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CONTENTS

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PAGE

No. 1. The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916), baboons of the African Plio-Pleistocene. C. J. Jolly 1

No. 2. Llandovery conodonts from the Welsh Borderland. R. J. Aldridge 125

No. 3. A revision of the Redfieldiiform and Perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). P. Hutchinson 233

No. 4. Lower Palaeozoic green algae from Southern Scotland, and their evolutionary significance. G. F. Elliott 355

No. 5. The Buchanosteid arthrodires of Australia. E. I. White & H. A. Toombs 377

No. 6. Planktonic foraminifera from the Palaeocene–Eocene succession in the Rakhi Nala, Sulaiman Range, Pakistan. B. K. Samanta 421

No. 7. *Megistotherium*, gigantic Hyaenodont from Miocene of Gebel Zelten, Libya. R. J. G. Savage 483

No. 8. Introduction to the Miocene mammal faunas of Gebel Zelten, Libya. R. J. G. Savage & W. R. Hamilton 513
[See also *Bull. Br. Mus. nat. Hist.* (Geol.), **21** (3) 1973 : 73–150]

Index to Volume 22 529

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THE CLASSIFICATION AND NATURAL HISTORY OF *THEROPITHECUS (SIMOPITHECUS)* (ANDREWS, 1916), BABOONS OF THE AFRICAN PLIO-PLEISTOCENE

C. J. JOLLY

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THE CLASSIFICATION AND NATURAL HISTORY OF *THEROPITHECUS (SIMOPITHECUS)* (ANDREWS, 1916), BABOONS OF THE AFRICAN PLIO-PLEISTOCENE

BY

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Pp. 1 – 123; 20 *Plates;* 32 *Text-figures*

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THE CLASSIFICATION AND NATURAL HISTORY OF *THEROPITHECUS (SIMOPITHECUS)* (ANDREWS, 1916) BABOONS OF THE AFRICAN PLIO-PLEISTOCENE

By C. J. JOLLY

CONTENTS

	Page
I. Introduction	4
II. Description of sites and material	8
A. Kanjera	8
Skull	8
Teeth	20
Forelimb	29
Hindlimb and Axial Skeleton	38
B. Olorgesailie	43
Skull	44
Teeth	45
Forelimb	46
Hindlimb	49
C. Olduvai, Upper Bed II Series	54
Skull	56
Teeth	59
Postcranial Material	59
D. Olduvai Bed I and Lower Bed II series	63
Skull	63
Teeth	63
Postcranial Material	64
E. Olduvai Bed IV Series	64
Skull	64
Teeth	65
F. Omo	66
G. Kaiso	67
H. Makapan	67
Skull	67
Teeth	68
I. Swartkrans	69
J. Hopefield	70

Page
III. THE AGE OF THE SIMOPITHECUS SITES 70
IV. THE SIZE OF SIMOPITHECUS 74
V. PHYLOGENY AND TAXONOMY 75
  A. Intrageneric Diversity 75
  B. Relationships of the Genus 87
    Taxonomic Summary of *Theropithecus* 94
VI. THE NATURAL HISTORY OF *Simopithecus* 97
  A. Habitat 99
  B. Anatomical Indications of Motor Habits 102
  C. Adaptations to Diet in the Dental and Cranial Anatomy of *Simopithecus* 111
VII. SUMMARY AND DISCUSSION 115
VIII. REFERENCES 116

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This paper is a revised version of part of a thesis presented in November 1964, in partial fulfilment of the requirements for the degree of Doctor of Philosophy at London University. The supervision and advice of Professor N. A. Barnicot and Dr J. R. Napier in the preparation of the thesis is gratefully acknowledged.

I. INTRODUCTION

The remains of large cercopithecoid monkeys are not uncommon in African Pleistocene and late Pliocene deposits, and many have been referred to extinct genera. One of the most frequently mentioned of these is *Simopithecus*. A thesis developed in this paper is that *Simopithecus* can be regarded as a subgenus of *Theropithecus*, a genus with a single extant species (*T. gelada*) confined to the high plateau of Central Ethiopia.

The earliest finds of fossil *Theropithecus* (= *Simopithecus*) were made by Dr Felix Oswald in 1911 at the site now known as Kanjera, close to the southern shore of the Kavirondo Gulf. Additional material was reported from the same site by Dr L. S. B. Leakey (1943a). Subsequent palaeontological explorations have documented the presence of the genus at almost all East African sites of Plio-Pleistocene age from which a representative fauna has been obtained: Olorgesailie (Cole, 1954; Isaac, 1966a), Olduvai (Hopwood, 1934, 1936; Leakey and Whitworth, 1958), Kaiso (Hopwood, 1939; Bishop, 1968), Omo (Arambourg, 1947; Howell, 1969), Koobi Fora (R. E. F. Leakey, 1970), and Lothagam (Patterson, Behrensmeyer and Sill, 1970). Freedman (1957) and Singer (1962) recount the discovery of the genus in South Africa, where it is known at Swartkrans, Makapan and Hopefield. Recognition of the genus at Ternifine, Algeria (Arambourg, 1962) extends its distribution to the extreme north of the African continent (Fig. 1). On the other hand, *Papio*

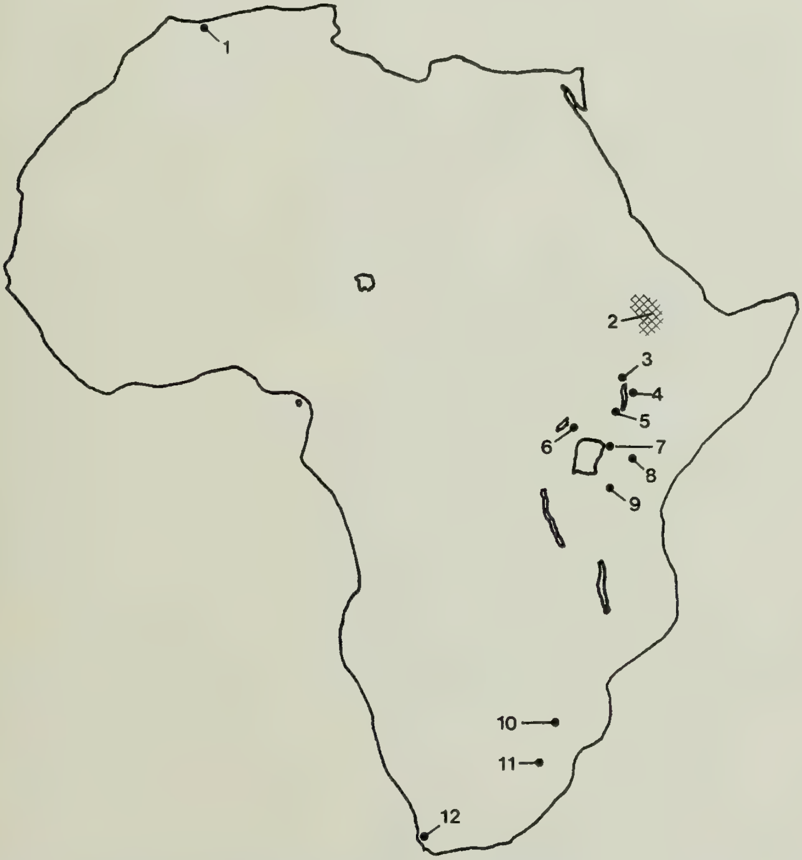

FIG. 1. Known occurrences of *Theropithecus*. 1. Ternifine. 2. *T. gelada*, present distribution. 3. Omo. 4. East Rudolf sites. 5. Lothagam, Kanapoi, Ekora. 6. Kaiso. 7. Kanjera 8. Olorgesailie. 9. Olduvai. 10. Makapan. 11. Swartkrans. 12. Hopefield.

(*Simopithecus*) *serengetensis* Dietrich 1942 from Laetolil, Tanzania, is almost certainly a *Papio* or *Parapapio* (Freedman, 1957). Leakey (1956) mentions postcranial fragments from Broken Hill, Zambia, which might be *Simopithecus*. While this is a possibility, the specimens might equally be derived from a *Papio* or other large, ground-living monkey.

Most of the material described in the literature consists of skulls, teeth, and cranial and dental fragments, but postcranial remains have been described by Andrews (1916) and Singer (1962).

The object of this study is to re-examine the taxonomy of the whole group, its relationship to other Cercopithecidae and its place in the Pleistocene ecosystem.

Original material from each of the East African sites was examined. This consisted of specimens previously mentioned or described (Andrews, 1916; Hopwood, 1934, 1936, 1939; Leakey, 1943a; Arambourg, 1947; Leakey and Whitworth, 1958) together with an extensive collection of material from Kanjera, Olorgesailie and Olduvai which had not been previously described. Much of this new material was unregistered at the time of writing. However, the considerable body of material from Olduvai described subsequent to 1961 was not included in the study, nor was the recently discovered material from Koobi Fora (R. E. F. Leakey, 1970). Both the series are currently under study by Dr Maeve Leakey. The very rich body of cranial, dental and postcranial material collected by the Chicago Omo Research Expeditions during 1968 and 1969 (Howell, 1969) was also unavailable at the time that the study was written. Assessment of the South African material was based largely upon detailed published accounts (Freedman, 1957, 1960; Singer, 1962) supplemented by casts of some of the material most generously made available by Mr Eric Delson.

The fossil material was compared with cranial and postcranial specimens of recent monkeys in the collections of the British Museum (Natural History), the Unit of Primatology and Human Evolution, Royal Free Hospital, and the American Museum of Natural History. Because skull form in the Cercopithecoidea is profoundly modified by allomorphosis (Reeve and Huxley, 1945; Freedman, 1962a, b), skull characters were compared primarily with the largest living monkeys; *Papio*, *Mandrillus* and *Theropithecus gelada*. *Macaca* was represented by one of its largest species, *M. nemestrina*. Each of the living Cercopithecinae used for comparison was represented by a substantial series in the British Museum collection.

Postcranial material used for comparison is listed in Table 1. This series represents the full range from the most arboreal (*Cercocebus albigena*) to the most terrestrial (*Theropithecus gelada*) of the living Cercopithecinae. Interpretations of skeletal features were checked by muscular dissections of cercopithecine limbs, as listed in Table 2.

Cranial specimens were measured for the most part following Freedman (1957). Four dimensions were recorded for each molar and three for each premolar tooth. Three molar dimensions (anterior and posterior breadth, length), are as defined by Freedman (1957). The fourth (estimated unworn length) is similar to length, but with a subjective correction for ante-mortem wear which is considerable in *Simopithecus*. Dimensions quoted from authors other than Freedman (1957) and Singer

TABLE 1

Cercopithecine comparative skeletal material

	Male	Female	?Sex	Wild-shot	Captive	History unknown	Adult	Subadult	TOTAL
Theropithecus gelada	3	—	—	—	3	—	3	—	3
Mandrillus	7	4	—	6	4	1	9	2	11
Papio	13	6	1	18	1	—	13	6	19
Cercocebus	4	1	—	4	1	—	4	1	5
Macaca	5	6	4	8	4	3	11	4	15
Cercopithecus	6	3	2	6	—	5	9	2	11
									64

TABLE 2

Muscular Dissections

	Sex	Age	Origin	Limbs Dissected
Presbytis entellus	M	Adult	Zoo	Fore
Papio cynocephalus I	M	Juvenile	Laboratory	Fore and Hind
P. cynocephalus II	M	Juvenile	Laboratory	Fore
T. gelada	M	Adult	Zoo	Fore and Hind
Cercocebus atys	M	Subadult	Zoo	Fore and Hind
Mandrillus sphinx	M	Subadult	Zoo	Fore and Hind

(1962) are usually of length and (maximum) breadth only, and perhaps differ slightly from the dimensions standardised by these authors and followed here.

Owing to sexual size dimorphism, it is necessary to distinguish specimens according to sex before comparisons in terms of size and statistical analysis are undertaken. Although it can be assumed that the biggest teeth in a variable sample will be male and the smallest female, the wide overlap between the sexes in dental size makes it impossible to sex the majority of specimens on size alone. Dental and cranial specimens were therefore sexed on morphological criteria. Specimens were thus allocated to one of three categories: *Male*, *Female* and *Unsexed*. For the sake of consistency, those specimens from South Africa which were sexed by Freedman on the grounds of size alone are here allocated to the *unsexed* group.

Mean, range, and sample variance (s^2) were calculated for each dental dimension for series of reliably sexed specimens. As *unsexed* teeth outnumber the other two categories in all cases except P_3, the overall range for all specimens from each site is also quoted. Descriptions of dental anatomy employ the terminology developed by Eric Delson for use in his forthcoming survey of cercopithecoid dentitions, and illustrated in Figs 2 and 3.

Postcranial specimens were compared with the modern series with especial reference to those features which have been found (Jolly, 1967) to be good indicators of terrestrial or arboreal adaptation. Measurements of two kinds were taken on postcranial material; those for calculations of indices of terrestrial adaptation, and others from which the unbroken lengths of the bones, and hence the general body-size of the animal and its limb-proportions, might be estimated.

Dental measurements were made with a sliding calliper equipped with a dial vernier and accurate to 0·1 mm. Cranial and postcranial dimensions were taken with sliding or spreading craniometric callipers graduated in millimetres.

In order to avoid excessive repetition, comparisons with other genera will be made in the body of the description of specimens, although general discussion is reserved for later sections.

II. DESCRIPTION OF SITES AND MATERIAL

A. KANJERA

The site of Kanjera, formerly known as Homa Mountain, is situated close to the southern shore of the Kavirondo Gulf of Lake Victoria. The earliest *Simopithecus* remains were recovered from the area in 1911 by Dr Felix Oswald (Andrews, 1916); extensive further collections were made by Dr L. S. B. Leakey (Hopwood, 1936, Leakey, 1943a; Leakey and Whitworth, 1958).

Kent (1942) describes the deposits as consisting of water-laid beds of volcanic ash, tuffs, and clays, and attributes their formation to a pluvial period. As well as a typical Middle Pleistocene fauna, the deposits contained pebble-tools and Acheulian hand-axes.

As a whole, the specimens from Kanjera are the best-preserved of the East African series. All are highly mineralised, hard and heavy. Surface detail of both bones and teeth is very finely preserved, there is no crumbling of the surface, and no evident post-mortem distortion, even in specimens consisting of almost complete skulls or mandibles. A very few specimens show damage due to weathering after surface exposure. The minimum number of individuals represented by the material is probably ten: four adult or sub-adult males, five adult or sub-adult females, and a juvenile female. Both cranial and postcranial skeletons are well represented.

Skull

The crania of both sexes and the female mandible are represented by almost complete specimens, the male mandible by more fragmentary examples.

a. F 3668 (Plate 3a and 4a)

An almost complete male cranium (figured in Leakey, 1943a; Leakey and Whitworth, 1958).

Apart from some damage to the lateral walls of the orbits, to the skull-base and to the right parietal region, the skull is virtually intact. All the permanent dentition is present, apart from the incisors, which are represented by stumps or empty alveoli. The tip of the left canine, and the lower half of the right, are also absent. The molars show some post-mortem damage. The third molars are not fully in occlusion, the posterior cusp-pair of both lying above the occlusal plane. The second molars and the pre-molars show moderate wear. The first molars show heavy wear, the dentine exposure on the occlusal surface being continuous over the whole tooth, obliterating the enamel infolding between the main cusp-pairs and also between these and the anterior and posterior projections.

The premaxilla is relatively small, with less bulging of the anterior surface over the roots of the incisor series than is seen in *Papio*, *Mandrillus* or *Macaca*, but rather more than in *Theropithecus gelada*. The inferior margin of the nasal aperture is much more horizontal than in *Papio*, *Macaca* and *Mandrillus*, and less pointed. Between the medial incisor roots, on the anterior face of the premaxilla, is an anteriorly-running groove, less deep than that seen in *Papio*, but deeper than that of the gelada. The lateral and inferior margins of the piriform aperture, apart from the region of the groove, are slightly raised and thickened, as is seen in some individuals of *Papio*, *Mandrillus* and *Macaca*. In *Theropithecus gelada* the lateral margins of the nasal aperture are sharp and not raised, and a pair of small, but prominent, conical tubercles are invariably present on either side of the midline on the inferior border. Probably these tubercles (mentioned by Vram, 1923) are associated with the cartilaginous support of the peculiar, upstanding external nose. The anterior surface of the premaxilla resembles that of *Papio* and *Macaca* in the ratio of its height to its width, rather than that of *Theropithecus gelada* which is higher and narrower. *Theropithecus gelada* also differs from the other monkeys examined, including *Simopithecus*, in the strong convexity of the anterior surface of its premaxilla. The skull agrees with the gelada, and differs from the other genera, in the very limited projection of the premaxilla anterior to the canines. The shape of the part of the premaxillary-maxillary suture visible on the surface of the palate resembles that of *Theropithecus gelada* more closely than those of the other genera in shape. The nasal processes of the premaxilla form the lateral margins of the piriform aperture, and extend on either side of it about 2 mm; much as in the modern species apart from *T. gelada*. In the latter, the nasal processes are very narrow and lie almost entirely within the aperture; this applies especially to the superior half of each process, which is narrowed by an abrupt angulation of the premaxillary-maxillary suture towards the midline. This feature is seen in all specimens of *Theropithecus gelada* and was distinguishable in an infant with full milk dentition, the youngest individual available.

The nasals are, relative to the size of the muzzle, very narrow; more narrow, absolutely, than in individuals of the other genera in which the whole muzzle is much less broad. The nasals are not raised above the smooth curve of the muzzle at any point in their length, unlike those of *Mandrillus*, which are always strongly raised, and *Papio*, in which they are usually raised. Those of *Theropithecus gelada* and *Macaca* are not raised, and resemble the condition in F 3668. The general contour of the nasals, as viewed from the lateral aspect, resembles that of *Papio* and *Theropithecus gelada*, with a sharp ante-orbital drop. The concavity of the facial profile is rather less than is seen in *Theropithecus*, and resembles that of *Papio*.

The flanks of the muzzle slope evenly from the midline to the alveolar margin, and are without the fossae seen in *Papio*, *Theropithecus gelada* and *Mandrillus*. In the gelada a deep maxillary fossa is present; this is outlined inferiorly by the inflated alveolar region covering the roots of the premolar and molar series and the flange joining this margin with the root of the zygoma; posteriorly by the deeply excavated malars which project abruptly from the surface of the muzzle, and superiorly by the slight angulation marking the border between the flank and the dorsum of the muzzle and the bulging of the maxillary surface over the root of the canine. In *Papio* and *Mandrillus* the elements forming the fossa are similar, but the ridge between the dorsum and the flank is more expanded, especially in *Mandrillus*, and in

Mandrillus and the larger forms of *Papio* the infraorbital excavation of the malar is less developed. In *Macaca* all the elements defining the maxillary fossa are absent, apart from a very slight expansion of the surface over the root of the canine and of the cheek-teeth. In the Kanjera specimen, the shape of the maxillary flank resembles that of *Macaca,* all the eminences outlining the fossa in the other genera being absent, apart from a slight expansion over the tooth-roots. The root of the zygoma runs smoothly into the surface of the maxillary flank without any appreciable angulation, and quite without excavation of its anterior surface. Two infra-orbital foramina are present on either side, close to the zygomatico-maxillary suture.

The supraorbital torus is shaped much as in *Papio, Mandrillus* and *Theropithecus gelada* and is rather more prominent than in most individuals of *Macaca.* It runs more or less horizontally across the brow, with only a slight, rounded depression separating its two halves; thus it contrasts in shape with the strongly-arched ridges seen in *Gorgopithecus* (Freedman, 1957, plate XLVIII). A supra-orbital notch is present, as in *Papio, Theropithecus gelada, Macaca* and *Mandrillus.*

The temporal lines, situated on the frontal bone, unite in the region of the bregma. Posterior to their point of union, a sagittal crest extends as far as the inion. In spite of minor damage to the crest, it can be seen that its highest point was at, or only slightly anterior to, the inion.

The shape of the calvarium resembles that of *Theropithecus gelada,* having a narrower post-orbital constriction than is found in the other modern genera. The nuchal crest is high, showing greater development than in any specimen of the modern series. In the temporal fossa, a prominent crest, situated on the part of the posterior wall of the orbit formed by the zygomatic bone, runs for several centimetres roughly perpendicular to the occlusal plane. This probably represents the anterior margin of the M. temporalis; in the gelada the crest is well-developed, in *Papio* it is present but less well-developed, while in *Mandrillus* its position is marked only by a rather weak line.

The anterior surface of the zygoma, as has been mentioned, is not grooved, ridged or excavated. Its general shape and the course of the zygomatico-frontal suture are as in *Papio* and the gelada. The zygomatic arches are evenly convex, enclosing broad temporal fossae, and are about as massive as in male individuals of *Papio* of comparable size. A conspicuous, roughened groove on the inferior surface, extending

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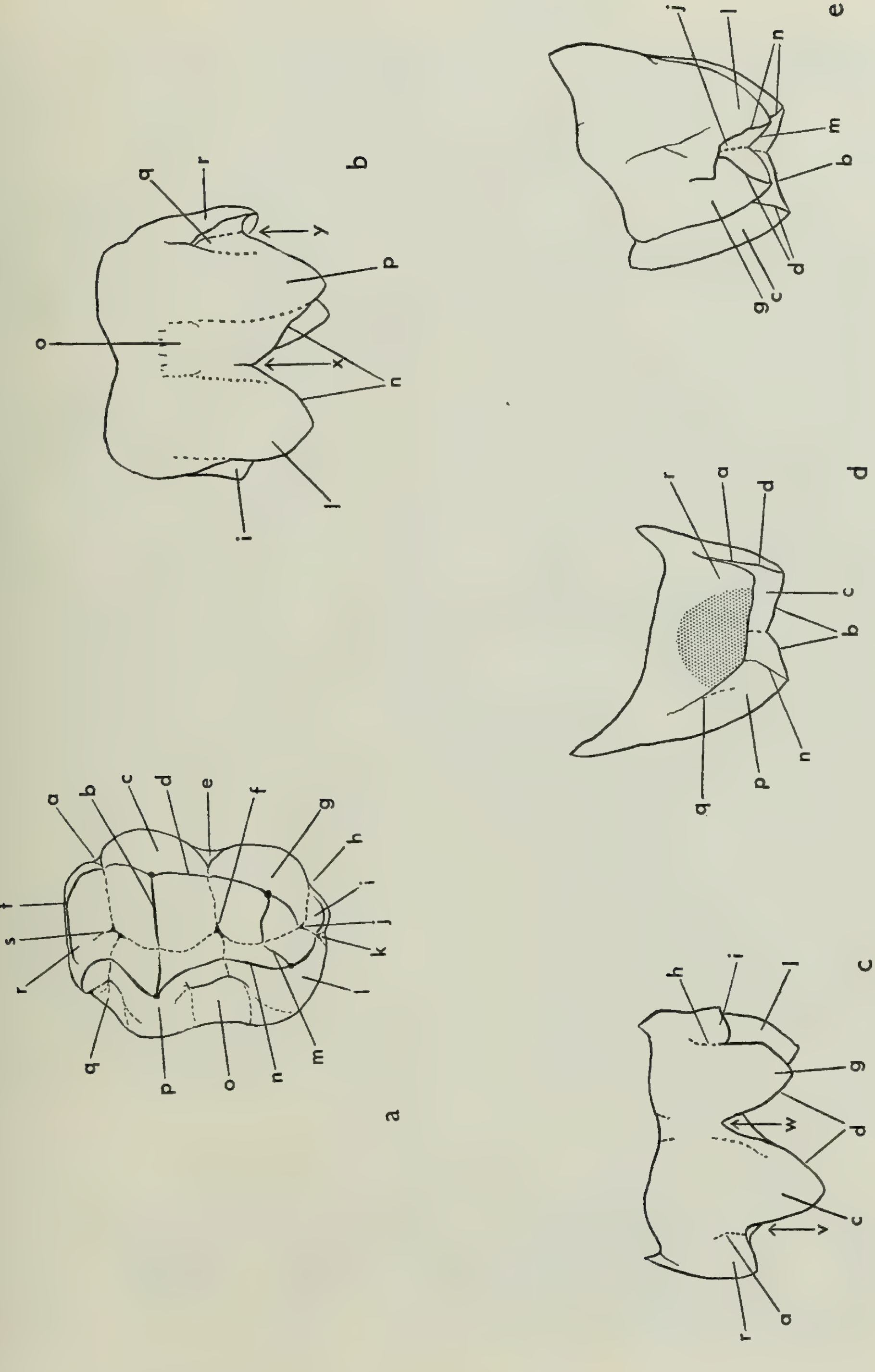
Fig. 2. Left, upper third molar of *T. gelada* to illustrate terms of dental anatomy used in this paper. A. Occlusal aspect. B. Lingual aspect. C. Buccal aspect. D. Mesial aspect. E. Distal aspect. a. Mesial buccal cleft. b. Protoloph. c. Paracone. d. Buccal margin. e. Median buccal cleft. f. Trigon basin. g. Metacone. h. Distal buccal cleft. i. Distal shelf. j. Distal fovea. k. Distal lingual cleft. l. Hypocone. m. Hypoloph. n. Lingual margin. o. Median lingual cleft. p. Protocone. q. Mesial lingual cleft. r. Mesial shelf. s. Mesial fovea t. Mesial margin. u. Distal buccal notch. v. Mesial buccal notch. w. Median buccal notch. x. Median lingual notch. y. Mesial lingual notch. Stippled area: contact facet for M^2. Grooves are represented by interrupted lines; crests and ridges by solid lines.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as far anteriorly as the angulation of the malar, represents the origin of the M. massetericus. Such a groove is present in the modern genera examined.

Viewed from the inferior aspect, the palate is more or less rectangular in outline, with the two stout canines standing at the anterior corners. There is, however, a distinct increase in the external breadth of the palate across the second molars, the tooth-row converging slightly both anterior and posterior to this. The two rather small anterior palatine foramina are situated in much the same position, relative to the tooth row, as in *Papio* and the gelada. The posterior palatine foramina are situated opposite the posterior cusps of the third molars; rather more anteriorly than in male specimens of *Papio* of comparable size and age; the feature is however a variable one. The anterior end of the vomer is preserved; this is thicker and stronger than the same element in any of the modern specimens.

Much of the base of the skull, including the part of the basi-occipital surrounding the foramen magnum, and most of both petrous temporal bones are missing; the external auditory meatus are however preserved, and it can be seen that they face rather more directly laterally, and less posteriorly and upwards than in *Papio*, *Theropithecus gelada* and *Mandrillus*. *Macaca* is rather closer to the fossil in this respect, having less posterior inclination than in the other recent genera, but in this genus too the meatus faces somewhat posteriorly. The mastoid area as a whole is somewhat raised above the level of the basi-occipital, as in most individuals of *Theropithecus gelada* and some *Papio* and *Mandrillus*. A rather prominent, conical true mastoid process is also present; this feature was found to be highly variable in the comparative series, both in degree of development and in distinctness from the surrounding surface. A process resembling that of this specimen of *Simopithecus* was found in at least one specimen of *Papio*, and in several *Macaca nemestrina*. None of the series of geladas or *Mandrillus* was found to have as well developed a mastoid process. The area of the mandibular articulation differs from that seen in *Papio* and *Mandrillus* in that it consists of two distinct surfaces, with an angulation between them. The larger and more lateral of these is transversely flat, but anteroposteriorly convex; the smaller, lying medial to the last, is convex in both dimensions and faces slightly laterally. In *Papio* and *Mandrillus* the articular surface is transversely evenly concave, but agrees with that of F 3668 in its anteroposterior convexity. In *Theropithecus gelada*, the condition resembles that seen in F 3668 but the smaller, medial face is less distinct, and less lateral facing. Both post-glenoid processes are absent, but the position of each can be distinguished. The lateral end of the external auditory meatus lies in contact with the post-glenoid process anter-

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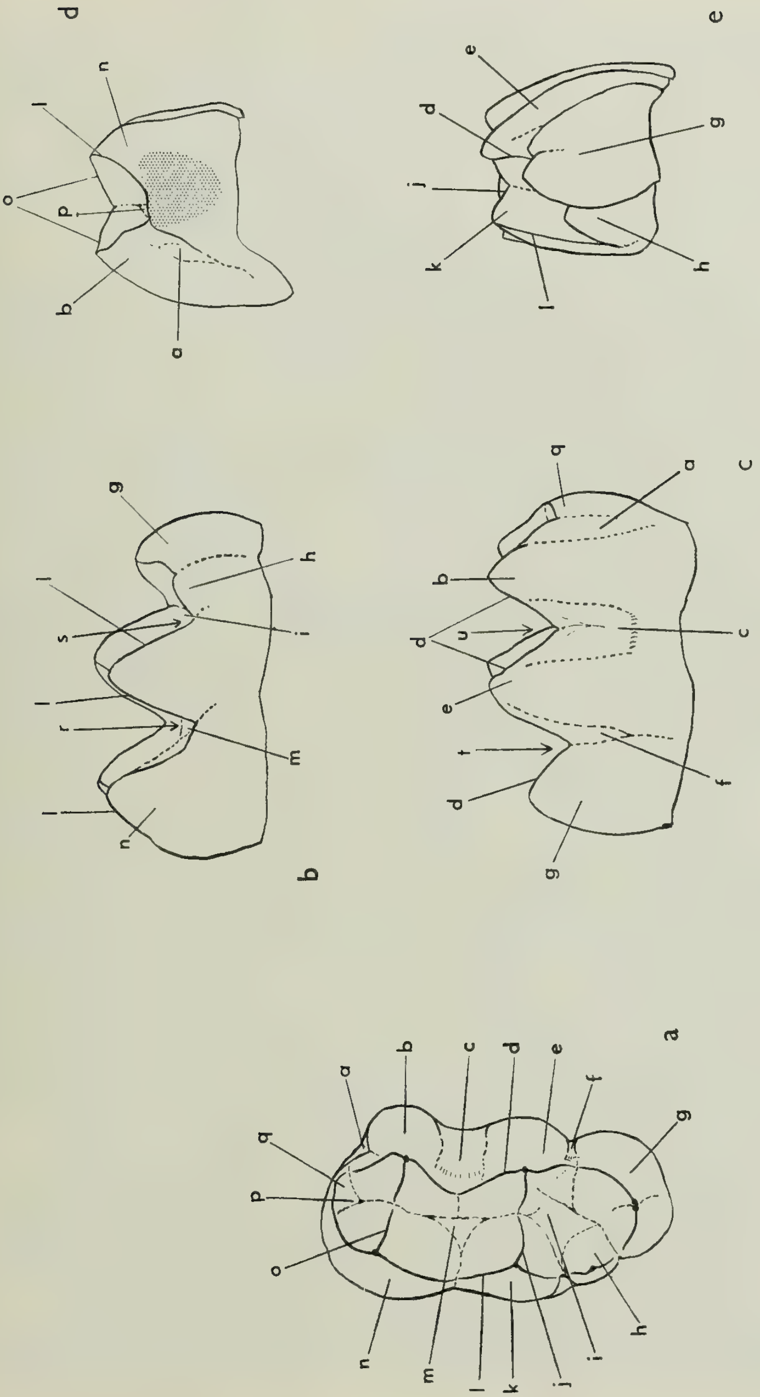
FIG. 3. Right, lower third molar of *T. gelada*. A. Occlusal aspect. B. Lingual aspect. C. Buccal aspect. D. Mesial aspect. E. Distal aspect. a. Mesial buccal cleft. b. Protocone. c. Median buccal cleft. d. Buccal margin. e. Hypoconid. f. Distal buccal cleft. g. Hypoconulid. h. Tuberculum sextum. i. Distal fovea. j. Hypolophid. k. Entoconid. l. Lingual margin. m. Talonid basin. n. Metaconid. o. Protolophid. p. Mesial fovea. q. Mesial shelf. r. Median lingual notch. s. Distal lingual notch. t. Distal buccal notch. u. Median buccal notch.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iorly, and the mastoid process posteriorly. This condition is not found in adults of *Papio*, *Mandrillus* or *Theropithecus gelada*, a distinct gap being invariably present between the meatus and the post-glenoid process. Some individuals of *Macaca* and *Cercocebus* have the meatus articulating with the post-glenoid process, and the condition seems to be regular in *Cercopithecus*, *Erythrocebus* and *Colobus*.

The basi-sphenoid is short and broad, as in *Theropithecus gelada*. Most of the basi-occipital is absent, but the sphenoid surface of the basal suture is intact, showing the latter to have been open at the time of death.

The pterygoid fossa is rather deep; it is divided into two by a ridge, beginning on the lateral wall of the medial pterygoid plate, running anterolaterally on to the medial wall of the lateral pterygoid plate, and ending in a tubercle on the free margin of the latter about a centimetre posterior to the palatine-maxillary suture.

b. M 14936 (Plate 5)

Reconstructed female skull (figured in Leakey and Whitworth, 1958).

Apart from the palatine and pterygoid region, which is mainly absent, and a small amount of damage to the lateral wall of the orbit and to the zygoma, the left half of the specimen is virtually complete. The missing regions have been in part restored in plaster of paris. The basal region, including the margins of the foramen magnum, is preserved, and the frontal is complete. On the right side, the upper part of the calvaria and parts of the region of the temporal fossa, including fragments of both the sphenoid and the temporal, are preserved, together with the post-glenoid process and the part of the temporal forming the root of the zygomatic arch. The more anterior parts of the right maxilla are also preserved. The rest of the right facial region, calvaria and zygoma have been reconstructed in symmetry with the left side, incorporating the fragments described.

On the left side, the molars and fourth premolar are preserved, together with the canine. The third premolar is represented by roots broken short at alveolar level. On the right side the molars and fourth premolar are again present, the former all showing some post-mortem damage. The canine is represented by a broken stump. None of the incisors is preserved, all being represented by roots or by empty alveoli. The individual evidently died shortly after reaching dental maturity; the third molars are fully erupted and in occlusion, with slight wear on all cusps. M^2 and P^4 show moderate, and M^1 extreme, attrition.

The premaxilla is somewhat damaged, the region of the inferior border of the nasal aperture being most affected. It can be seen that it was of the same general shape as in the male specimen; relatively rather small, scarcely projecting anteriorly beyond the canines; the lateral margins of the piriform aperture are somewhat raised and thickened, again as in the male specimen.

The muzzle slopes evenly from the midline to the alveolar margin, with only the slightest angulation between the dorsum and the flanks. The very slight maxillary depression is formed by the low inflation over the canine root and the buccal roots of M^1, both of the latter being exposed. The shape of the zygomatic root, sweeping into the surface of the flank of the muzzle without a distinct angulation, resembles the condition seen in the male specimen. The zygomatic arch itself is stout and strongly bowed. The areas of origin of the M. massetericus are deeply grooved and ridged, especially at malar angle, where, as in the male specimen, a distinct tubercle is present. The mandibular articular surface is antero-posteriorly narrow and convex. and evenly concave transversely; thus it resembles the normal shape in the modern Cercopithecinae more than does F 3668. The post-glenoid process is both longer and stouter than in any of the modern series. The skull-base is relatively broad. The external auditory meatus is directed as in the male specimen, more directly laterally than in the modern genera. The hypoglossal, jugular and carotid foramina are visible on the right side. All lie very close together, and the hypoglossal foramen is scarcely visible from directly below, being concealed by the occipital condyle. The posteromedial wall of the foramen ovale is absent; the antero-lateral wall is formed of the sphenoid. The left mastoid region is preserved; a prominent, conical mastoid process is present. As in the male specimen, the external auditory meatus is in contact with both the mastoid process and the post-glenoid process.

The supra-orbital ridge resembles that of the male specimen. The superior and inferior temporal lines of each side are close together, forming a raised ridge. The superior lines meet exactly at the bregma; the inferior lines come close to meeting in this region, but then run almost parallel for most of the length of the sagittal suture, finally meeting about 4 cm anterior to the inion. Posterior to their point of meeting a low sagittal crest is formed. The nuchal crest is present as a flange, lower than that of the male, but higher than in females of the modern genera, which reaches its maximum development lateral to the inion. No prominent external occipital protuberance is present.

c. A fragmentary female skull (unregistered) (described by Leakey, 1943a), reconstructed in plaster. The parts preserved include the frontal, a fragment of the cranial vault, mainly of the right side but including the region of the inion; the right zygomatic and most of the maxilla of the same side, as far anteriorly as the alveolus of P^3, part of the left zygomatic, including the malar angle; and the part of the left zygomatic arch formed by the temporal bone. The complete dentition is present, $M^3 - P^3$ of the right side in their alveoli, the rest of the teeth set in plaster. The third molars were about to come fully into occlusion at the time of death, with noticeable wear only on the extreme tip of the antero-buccal cusp. The specimen was therefore slightly younger at the time of death than the male described above. The maxillo-zygomatic and zygomatico-temporal sutures are more obviously open and loosely-knit than those of the previously-described female specimen.

The shape of the facial region is very much as described for the previous female specimen. The reconstruction of the skull probably errs in making the anterior border of the premaxilla too broad and flat, underestimating the convergence of the anterior ends of the tooth-rows. Three infra-orbital foramina are present in the preserved maxilla, immediately adjoining the maxillary-zygomatic suture. A zygomatico-facial foramen is also present, at the level of the inferior border of the orbit. The superior and inferior temporal lines are similar to those of the last specimen. They are prominent in the region of the temporal fossa, sweeping together and almost meeting at the bregma. The superior temporal lines meet slightly posterior to the bregma (this region is somewhat damaged); the inferior temporal lines do not meet, but run parallel, about 5 mm apart, and then diverge on approaching the nuchal line. Both lines are visible in the region of the inion, meeting the nuchal crest about 12 mm apart.

d. Unregistered

The right glenoid region of a skull, with a complete post-glenoid process (figured in Leakey and Whitworth, 1958.)

The post-glenoid process is extremely stout and long. The morphology of the rest of the fragment resembles that of F 3668; it is slightly larger than the corresponding reigon of the latter, and therefore probably represents a fully adult individual.

e. M 11537 (Plate 7c and d)

An almost complete muzzle region, with both maxillae, and part of the zygomatic bones of both sides present, rather more on the left than on the right side. Also a very small part of the left premaxilla, forming the inferior lateral margin of the piriform aperture. On the left side, the cheek-tooth row is complete; on the right, all the molars and premolars and the canine are present. In the premaxillary fragment, the roots of the left incisors are visible. All cheek-teeth, apart from M^3 and P^3, show rather extreme wear. From the small size of the canine, the specimen is obviously female.

The shape of the flanks of the muzzle agrees exactly with the condition seen in the female specimens described above; the very slight hollowing of the maxillary surface is due entirely to a small swelling of its wall over the roots of the molars. The bone covering the buccal roots of the molars is extremely thin, and some of the latter are in part exposed. The shape and orientation of the zygoma is exactly as in the other female specimens, without fossae or distinct angulation. With the occlusal plane horizontal, the most inferior point of the zygomatic root lies above the anterior cusps of the third molar.

f. M 18720 (Plates 6c and 7a and b)

A complete premaxilla, with adjoining parts of the left and right maxillae, to the level of P^4. Both left, and the lateral right incisors are present. All premolars are present, and show slight wear. The small size of the canines shows the specimen to be female.

A deep medial groove is present between the incisors; apart from this region, the premaxillary part of the inferior and lateral margins of the piriform aperature is slightly raised, confirming the condition seen in the more complete male and female skulls described above. Almost certainly from the same individual as:

g. M 11538 (Plate 7a and b)

The posterior part of a maxilla, with the molars preserved. The first and second molars show slight to moderate wear; the third is fully erupted and in occlusion, but shows very slight wear on the anterior pair of cusps only. The maxillary surface, as in the other specimens, is smooth, without a fossa. The roots of the molars are covered by only a thin layer of bone; both the buccal roots of M^1, and the anterior buccal root of M^2 are exposed. Four infra-orbital foramina are present, all situated on the maxillary-zygomatic suture. Three are situated close together in a single pit in the maxillary surface. The posterior palatine foramen is visible, opposite to the posterior cusps of the third molars.

h. M 18767

Part of a cranial vault, mainly of the right side; includes the posterior part of the parietal, with the inion and sagittal crest preserved, together with a small part of the temporal.

The structure of the sagittal crest resembles that seen in the more complete specimens.

Registered under the same number is a fragment of the frontal from the right supra-orbital region, including the superior surface of the orbit. The superior and inferior temporal lines are so close together as to give the impression of a single, raised line. Judging from the close approach of the line to the midline of the vault, it probably met its fellow anterior to the bregma.

i. M 18765 (Plate 4b)

Frontal fragment, together with the extreme upper parts of the nasals. The supra-orbital tori are mostly absent, but the glabella region preserved. The temporal lines are prominent, converging to meet well anterior to the bregma. The two lines are asymmetrical, that of the right reaching rather higher on to the cranial vault than that of the left.

j. M 18764 (Plate 8a and b)

Part of the superior surface of the cranial vault, together with a small part of the nuchal surface. The temporal lines converge to a point anterior to the bregma, posterior to which a rather high sagittal crest is present. Although the free margin of the crest is somewhat damaged, it can be seen that its highest point was probably anterior to the inion.

k. M 18766

Two fragmentary frontal bones. Both show a pattern of development of the temporal lines similar to the specimens described.

l. F 3394 (Plate 4c)

An almost complete frontal, only slightly damaged by surface erosion. The shape of the supra-orbital region and the pattern of the temporal lines agrees with the specimens described. The temporal lines converge to meet almost exactly at the bregma.

m. M 11539 (Plates 9b and 10a)

An almost complete female mandible (Type of *S. oswaldi* Andrews; figured by Andrews 1916, Leakey and Whitworth, 1958).

The specimen is complete apart from the gonial region of either side and the right coronoid process. On the left side the molar and premolars are all present; on the right, the molars are preserved, but the premolars are broken off at alveolar level. The incisors are represented by broken stumps or roots.

The third molar is fully erupted, in occlusion and shows light wear, the central 'bridge' between the cusp-pairs being unopen. The remaining cheek-teeth show moderate or heavy wear.

The corpus is more robust than in females of *Papio* and *Theropithecus gelada* and there is only the slightest trace of a mandibular fossa, immediately posterior to the canine and below the premolars. The anterior surface is not grooved and ridged by the roots of the incisors, as in *Papio*. Four mental foramina are present, situated below P_4 and the anterior cusps of M_1. The internal surface of the symphyseal region may be described in terms of an upper and a lower shelf, connecting the two halves of the mandible, and a pit on the internal aspect of the symphysis which separates the two shelves. The superior shelf extends backwards to the level of the posterior margin of the fourth premolar, further than in females of *Papio* (in which it extends approximately to the level of the posterior margin of the third premolar) and *Theropithecus gelada*, in which it reaches approximately the midpoint of P_4. Its superior surface is much less excavated than in any modern cercopithecoid genus. With the occlusal plane horizontal, the inferior ('simian') shelf extends posteriorly as far as the rear of the first molar, again more extensively than the corresponding shelf in *Papio* and *Theropithecus gelada*. The gonial region is mainly absent, but it is apparent that the bone thins rather abruptly posterior to the position of the roots of the molars, and that the gonial angles themselves were inverted, as in the modern forms.

The anterior margin of the ascending ramus bears, near its base, a prominent tubercle, which represents the area of attachment of the tendinous part of the insertion of M. temporalis. The coronoid process is strong. Immediately below it, on the lateral surface, is a conical tubercle, pierced by a foramen; this is presumably pathological in origin, since it is absent in all individuals of the comparative series, and in the other *Simopithecus* specimens in which the region is preserved. On the internal aspect, a raised crest runs upwards to the base of the coronoid process; this ridge, which is present in *Theropithecus gelada*, but not in *Papio* or *Macaca*, probably marks the limit of the extent of the insertion of M. temporalis on the internal aspect.

The articular surface of the condyle is rather flat, demarcated by a lip, and shows the lack of lateral expansion mentioned by Leakey and Whitworth as characteristic of the genus. On the posterior surface, immediately below the articular surface, is a distinct depression. As preserved, the angulation of corpus to ramus is somewhat less steep than in *Theropithecus gelada* though steeper than in *Papio* of comparable size. The angular region is somewhat damaged, however, and may be distorted in reconstruction. In any case, the ramus of the mandible belonging to M 14936 must have been both higher and more vertical.

n. F 3398 (Plates 9c and 10b)

A juvenile female mandible, complete apart from the coronoid processes, and the posterior margin and condyle of the right ascending ramus (described by Leakey, 1943a).

The dentition is almost complete. The incisors and canines are present and well-preserved. P_3 is fully erupted, and its tip is slightly worn. The tip of P_4 is just emerging from the alveolus, and the left is still covered by the milk-molar. M_1 is fully erupted, and shows wear on all its cusps, but the waist of dentine between the anterior and posterior cusp-pairs is not open. M_2 has reached a stage of eruption where the anterior cusps are in the occlusal plane, but show no wear; the posterior cusps are still below this level. M_3 had not started to emerge from the alveolus at the time of death, but the germ of the crown of the left M_3 has been dissected from its crypt.

As might be expected in a juvenile individual, the mandibular corpus is lower and more lightly-built than that of the adult female specimen, M 11539. The inferior surface of the symphysis is flat. The two shelves on the internal aspect of the symphysis are less backwardly-extended relative to the dentition than in the adult individual; the superior shelf extends back as far as the posterior cusps of the third premolar, the inferior shelf to the level of the posterior margin of the fourth premolar. The very shallow excavation of the superior surface of the upper shelf, however, resembles the adult condition. The external surface of the corpus is without a fossa. From the lateral aspect, the inferior margin of the corpus is slightly expanded in the region of the insertion of the M. masseter. The bone becomes thin in the gonial region, which is slightly inverted, and bears three tubercles on its internal surface. The lipping of the articular surface of the condyles, and the depression on the posterior surface, resemble the condition described in the adult, but the internal expansion of the articular surface is less pronounced.

o. M 18770

A mandibular fragment, consisting of the posterior part of the corpus, without the gonial region. The roots of the third molar, a worn and broken second molar, and a fragment of the posterior root of the first molar are present. This fragment confirms the robusticity of the corpus, and the thinning of the bone towards the gonial region, observed in the previous specimens.

p. M 11541 (Plates 9a and 10c)

A fragment of a left, adult mandibular corpus, with P_4–M_3 present. The first molar is broken; the second shows moderate to heavy, and the third moderate attrition. P_4 is moderately worn.

The features of this specimen resemble those of M 11539, except that the inferior margin below M_1 and P_4 is slightly flared laterally, so that a shallow mandibular fossa was probably present.

q. M 19011 (Plate 8c and d)

A fragment of a right mandibular corpus, with P_3–M_2. The small size of the P_3 indicates a female individual. P_3 is newly erupted, with only very slight wear on the tips of the cusps. P_4 is moderately worn, M_1 shows heavy, and M_2 moderate to heavy wear. The inferior margin and the inferior half of the corpus is absent, but the outline of the superior symphyseal shelf is visible. This extends posteriorly as far as the posterior part of P_4, as in M 11539.

r. M 19012

The left ascending ramus of a mandible, complete except for the margin of the notch and the coronoid process. No teeth are present, but the impression of the posterior root of M_3 can be seen on the anterior, broken, surface of the fragment. The position of this shows that the individual was probably adult at the time of death. The details of the condyle resemble those described in M 11539, with lipping and the posterior fossa, but again the internal expansion of the articular surface, though more pronounced than in the modern forms, is less great than in M 11539. The bone of the gonial region is thin, with very slight inferior expansion of the area of insertion of the M. masseter. The margin is somewhat inverted, and three promiment tubercles, representing the area of insertion of the M. pterygoideus internus, are present. The area of temporal insertion is as described for M 11539, but the fossa is slightly deeper.

s. Unregistered

A fragment of the symphyseal region of a male individual, including the inferior surface, part of the internal surface, and the posterior surface of the alveoli of the canines.

The inferior surface of the symphysis is flat. The alveoli of the canine roots are close together at their inferior ends, and then diverge; the space between them for the incisors is relatively narrower than in any of the modern forms. Three mental foramina are present, near the inferior margin of the corpus.

t. Unregistered

An isolated right mandibular condyle (figured in Leakey and Whitworth, 1958). The morphology of this specimen, which from its size is almost certainly male, resembles that of the specimens described above. The internal extent of the articular surface resembles the condition seen in M 19012 and F 3398.

Teeth

The characteristic features of the molars and premolars of *Simopithecus* have been described in some detail by Leakey and Whitworth (1958), Freedman (1957) and Singer (1962), and are best appreciated by reference to the illustrations (Figs. 2, 3; Plates 6–10). The molars of both sexes, when compared to those of large Cercopithecinae of other genera appear large, and, when unworn, distinctly hypsodont, with strong contrast between the high, columnar cusps and the deep fovae.

One of the more distinctive features is commonly described (Leakey and Whitworth, 1958) as a high, longitudinal ridge connecting hypoconid and protoconid in the lower molar, and protocone and hypocone in the upper. This feature is in fact due to modifications in structures which are present in all cercopithecine molars, rather than the appearance of a new structure. Upper molars are in this respect mirror images of lower which are described here.

First, the talonid basin itself is deep, with a comparatively horizontal floor and vertical buccal face. This buccal face forms the lingual wall of the 'buccal longitudinal ridge'. On the buccal side, the median buccal cleft is deep, and is also bounded by comparatively vertical faces. Its lingual face forms the buccal wall of the longitudinal ridge. The supposedly distinctive appearance of the worn *Theropithecus* (*Simopithecus*) molar occurs when wear has reached the stage at which the occlusal surface is at the level of the base of the median buccal notch. At this stage of wear, a dentine 'bridge' opens between the lakes of dentine representing the truncated bases of the protoconid, metaconid and protolophid (mesially) and the hypoconid, entoconid and hypolophid (distally). The single dentine lake now has an asymmetrical hour-glass form, with the central bridge running along the crest of the buccal margin. All cercopithecine molars will pass through this stage of wear, and will show the hour-glass pattern of dentine exposure with a median longitudinal ridge until the floors of the talonid basin and the median buccal cleft lose their enamel. Since the cusps are high, and the floors of the foveae relatively low, in *Simopithecus* this stage is more prolonged than in other Cercopithecinae.

The lingual margin of the lower molars is no higher than in other Cercopithecinae, so that the flat-floored talonid basin appears to be broadly open lingually. It is, however, defined lingually by a ridge upon which are usually one or more cuspules. A similar condition is characteristic of the trigon basin in the upper molars, which is distinctively open bucally and bounded by the comparatively low buccal margin. The mesial fovea is also deep, and extends mesio-lingually as a deep fissure partially encircling the base of the metaconid, separating the latter cusp from the mesial shelf, which is thus demarcated as a prominent almost loph-like ridge connected to the protoconid. The mesial end of the tooth is further demarcated by the mesial buccal groove, which, while present in other large Cercopithecinae, is deeper and wider in *Simopithecus*. With wear, dentine exposure spreads mesio-lingually along the ridge from the protoconid, as in other Cercopithecinae and also, distinctively, mesio-*buccally* along the crest of the ridge defined by the deep mesio-buccal grove. At this stage of wear, therefore, the *Simopithecus* tooth presents a distinctive appearance, from the occlusal aspect, with a subsidiary area of exposed dentine in the shape of a symmetrical letter T connected to the protoconid- metaconid-protolophid dentine lake by its stem.

In the upper molars, precisely complementary peculiarities are seen in the mesial end of the tooth. The mesial fovea is deep, and the mesial lingual groove, which is variably but weakly developed in other large Cercopithecinae, is deep and extensive, so that the distinctive T-shape appears with wear.

Similar modifications are seen at the distal end of the tooth. In lower M_1–M_2 the floor of the distal fovea is low and broad, and the fovea itself opens lingually through a deep distal lingual notch. On the buccal side the distal buccal groove is deep. In the upper molars, the distal fovea opens through a deep distal buccal notch, and the distal lingual groove, which is weak or absent in large Cercopithecinae of other genera is deep.

Mesially, the lower M_3 is similar to M_1 and M_2. However, as in all Cercopithecinae apart from the tribe Cercopithecini, it bears a hypoconulid on the margin of its distal shelf, in line with, or slightly lingual to, the line connecting protoconid and hypoconid. As in M_1 and M_2, the distal fovea is deep, and its lingual margin is low. No examples were found with a tuberculum sextum (Swindler et al., 1967) approaching the hypoconulid in size. However, the flat, low floor of the distal fovea is crossed by grooves which define low cusplets along its raised margin. The distal buccal groove is again relatively broad and deep, and, like the median groove, its steep lingual wall, and that on the buccal side of the distal fovea define, between them, a continuation of the 'buccal longitudinal ridge' from hypoconid to hyperconulid.

P_3 is of the usual form for Cercopithecoidea; it is a unicuspid tooth whose predominant feature is the long, plane, sectorial face sweeping mesio-buccally from the summit of the protocone. The development of this face is clearly sexually dimorphic, the male being much the larger. However, compared to similarly sized males of *Papio*, and still more *Mandrillus*, the sectorial face is short relative to the length and breadth of the talonid. The talonid basin, on the other hand, is large. In females, the deviation from the condition in other large Cercopithecinae is much less noticeable.

P^3 and P^4 are very similar in structure, although P^4 is distinguished by its more symmetrical outline, its lingual margin being more nearly equal to the buccal than in P^3. They differ from their homologues in other large Cercopithecinae principally in having rather deeper basins, and by exhibiting two vertical grooves on the lingual surface, one mesial, the other distal to the protocone. On the buccal side, P^4, especially, hows traces of similar grooves defining a column topped by the paracone. The canines show considerable sexual dimorphism. Female upper and lower canines are not dissimilar from the equivalent teeth in other large Cercopithecinae although they appear small by comparison with the large cheek teeth. The male upper canines, however, even when relatively unworn as in F 3668, are much less high crowned than those of male *Papio*, *Mandrillus* and *Theropithecus gelada*, both in comparison with the size of the animal, and with the robusticity of the canine itself. The flange which runs from the distal buccal corner of the tooth-crown to its tip, and which, when honed against the sectorial face of P_3, bears a sharp cutting edge, is less distinct that in *Papio*, and much less than in *Mandrillus*. The male lower canine is represented by the isolated, worn specimen M 18729. Its unworn height cannot be reconstructed.

The male upper incisors are not known, but to judge from the size and orientation of their roots in F 3668, they must have been relatively small and vertically-placed.

TABLE 3

Cranial Dimensions in *Theropithecus*

	No. in descriptive list	Sex	Greatest Length	Prosthion-Glabella	Inion-Glabella	Post-orbital Constriction	Basion-Prosthion	Basion-Bregma	Temporal Breadth	Mastoid Breadth	Inion-Basion	Muzzle breadth at M^2	Bizygomatic Breadth
T. gelada series													
Mean ±	—	M	172·8	94·5	105·0	41·9	126·2	67·4	72·3	83·1	53·2	48·1	110·4
Variance			±	±	±	±	±	±	±	±	±	±	±
(N=13)			42·5	48·4	11·2	4·1	32·5	3·8	7·5	4·5	4·5	6·4	9·8
T. gelada,													
Mean of 2		F	158·5	81·0	97·5	43·0	111·5	62·0	68·5	78·5	50·0	45·0	—
Kanjera													
F 3668	a	M	207·0	114·0	125·5	47·0	—	—	83·0	100·0	—	60·0	134·0
M 14936	b	F	172·0	88·0	118·0	50·0	114·0	70·5	79·0	87·0	54·0	56·0	116·0
M 11537	e	F	—	—	—	—	—	—	—	—	—	53·0	—
Olduvai													
Bk II 1957	d	F?	—	—	128·0	56·0	—	76·0	85·0	106·5	62·5	—	—
Swartkrans													
SK 561*	—	F	—	(90)	—	47·0	—	—	—	—	—	—	—
Hopefield													
8400**	—	?	—	—	121·5	50·0	—	—	—	94+	—	—	—

* from Freedman, 1957.
** from Singer, 1962.
+ 'Maximum bi-auricular breadth', which is probably close to mastoid breadth (98·5 in F 3668).

A similar reduction in the lower incisors in the male is indicated by the extremely small space between the alveoli of the canines in the mandibular fragment (s., above). In the female, the upper incisors are well-preserved in M 18720, where it can be seen that they were, even when unworn, considerably smaller than those of other large Cercopithecinae, relative to the size of the animal. The lower incisors, finely preserved in F 3398, are also small and slender.

The dimensions of the cheek-teeth are shown in Table 4.

TABLE 4

Dimensions of Cheek-Teeth in *Theropithecus*

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
P^3 *Breadth*										
Theropith. gelada	10	7·15	6·4– 8·0	0·176	1	6·2	—	—	11	6·2– 8·0
Kanjera	1	10·7	—	—	2	8·7	8·6– 8·8	—	3	8·6–10·7
Olorgesailie	—	10·5	—	—	—	—	—	—	12	9·6–10·7
Makapan	—	—	—	—	1	7·7	—	—	1	7·7
Swartkrans	—	—	—	—	3	9·3	8·9–10·0	0·240	5	8·9–10·0
P^3 *Length*										
T. gelada	10	6·4	6·2– 6·8	0·038	1	4·9	—	—	11	4·9– 6·8
Kanjera	1	8·0	—	—	2	6·7	6·4– 7·0	—	3	6·4– 8·0
Olorgesailie	1	8·5	—	—	—	—	—	—	12	8·1–10·4
Makapan	—	—	—	—	1	5·7	—	—	1	5·7
Swartkrans	—	—	—	—	3	8·0	6·0– 9·6	2·240	5	6·0–11·3
P^3*EUL*										
Kanjera	1	8·4	—	—	2	7·4	7·2– 7·6	—	3	7·2– 8·4
Olorgesailie	1	8·5	—	—	—	—	—	—	12	8·1–10·4
P^4 *Breadth*										
T. gelada	10	7·7	7·0– 8·7	0·294	1	6·6	—	—	11	6·6– 8·7
Kanjera	1	10·8	—	—	3	9·8	9·6– 9·9	0·02	3	9·6–10·8
Olorgesailie	1	13·7	—	—	—	—	—	—	6	11·0–13·7
Makapan	—	—	—	—	2	8·7	8·6– 8·8	—	2	8·6– 8·8
Swartkrans	—	—	—	—	3	9·9	9·0–10·6	0·435	6	9·0–10·7
P^4 *Length*										
T. gelada	10	6·86	6·1– 7·3	0·123	1	5·7	—	—	11	5·7– 7·3
Kanjera	1	8·7	—	—	3	7·9	7·7– 8·1	0·09	3	7·7– 8·1
Olorgesailie	1	8·5	—	—	—	—	—	—	6	8·5–10·4
Makapan	—	—	—	—	2	7·65	7·5– 7·8	—	2	7·5– 7·8
Swartkrans	—	—	—	—	3	8·1	7·3– 9·2	0·63	6	7·3– 9·5
P^4*EUL*										
Kanjera	1	9·4	—	—	3	8·6	8·3– 8·7	0·04	3	8·3– 8·7
Olorgesailie	1	8·5	—	—	—	—	—	—	6	8·5–10·4

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M^1 Anterior Breadth										
T. gelada	10	9·1	8·7– 9·4	0·059	—	—	—	—	10	8·7– 9·4
Kanjera	1	12·8	—	—	3	10·5	10·2–11·0	1·51	6	10·2–12·8
Olorgesailie	1	15·3	—	—	—	—	—	—	8	13·2–15·3
Makapan	—	—	—	—	1	9·9	—	—	1	9·9
Swartkrans	—	—	—	—	3	11·26	10·9–12·0	0·284	4	10·9–12·0
Hopefield	—	—	—	—	—	—	—	—	2	9·9–14·0
M^1 Posterior Breadth										
T. gelada	10	8·5	8·1– 9·1	0·074	—	—	—	—	10	8·1– 9·1
Kanjera	1	12·3	—	—	3	10·0	9·8–10·3	0·06	6	9·8–12·3
Olorgesailie	1	14·7	—	—	—	—	—	—	8	12·9–14·7
Makapan	—	—	—	—	1	9·4	—	—	1	9·4
Swartkrans	—	—	—	—	3	10·4	9·9–10·6	0·126	4	9·9–10·6
Hopefield	—	—	—	—	—	—	—	—	2	9·5–12·5
M^1 Length										
T. gelada	10	10·5	9·9–11·2	0·156	—	—	—	—	10	9·9–11·2
Kanjera	1	13·1	—	—	3	10·8	10·4–11·1	0·086	6	10·4–13·1
Olorgesailie	1	15·5	—	—	—	—	—	—	8	15·5–17·5
Makapan	—	—	—	—	1	12·0	—	—	1	12·0
Swartkrans	—	—	—	—	3	13·2	12·0–15·1	1·913	4	11·7–15·1
Hopefield	—	—	—	—	—	—	—	—	2	12·0–14·0
M^1 EUL										
Kanjera	1	14·0	—	—	3	12·8	12·5–13·1	0·079	6	12·5–14·0
Olorgesailie	1	16·5	—	—	—	—	—	—	8	16·1–17·6
M^2 Ant. Breadth										
T. gelada	10	11·0	10·0–11·6	0·166	1	9·7	—	—	11	9·7–11·6
Kanjera	1	14·8	—	—	3	12·8	12·3–13·0	0·235	5	12·3–14·8
Olorgesailie	—	—	—	—	—	—	—	—	10	15·0–19·0
Makapan	—	—	—	—	—	—	—	—	2	13·3–14·9
Swartkrans	—	—	—	—	3	13·9	13·6–14·5	2·00	5	13·6–14·9
Kaiso	—	—	—	—	—	—	—	—	1	12·5
M^2 Post. Breadth										
T. gelada	10	9·8	9·3–10·3	0·146	1	8·5	—	—	11	8·5–10·3
Kanjera	1	14·2	—	—	3	11·7	11·4–12·2	0·194	5	11·4–14·2
Olorgesailie	—	—	—	—	—	—	—	—	10	13·5–17·4
Makapan	—	—	—	—	—	—	—	—	2	12·8–13·6
Swartkrans	—	—	—	—	3	12·66	12·3–13·2	0·318	5	12·3–13·3
Kaiso	—	—	—	—	—	—	—	—	1	12·0
M^2 Length										
T. gelada	10	12·8	11·4–13·7	0·522	1	11·0	—	—	11	11·0–13·7
Kanjera	1	17·7	—	—	3	14·4	14·2–15·1	0·249	5	14·0–17·7
Olorgesailie	—	—	—	—	—	—	—	—	10	18·7–22·3
Makapan	—	—	—	—	—	—	—	—	2	16·8–17·9
Swartkrans	—	—	—	—	3	17·3	16·6–18·1	0·380	5	15·9–18·1
Kaiso	—	—	—	—	—	—	—	—	1	15·4

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M^2 EUL										
Kanjera	1	18·1	—	—	3	15·5	15·2–15·8	0·060	5	15·2–18·4
Olorgesailie	—	—	—	—	—	—	—	—	10	18·9–23·0
Kaiso	—	—	—	—	—	—	—	—	1	16·3
M^3 Ant. Breadth										
T. gelada	9	11·1	10·2–12·4	0·326	1	9·2	—	—	10	9·2–12·4
Kanjera	1	14·3	—	—	3	13·2	12·9–13·5	0·148	6	12·9–14·3
Olorgesailie	—	—	—	—	—	—	—	—	8	15·7–18·0
Makapan	—	—	—	—	—	—	—	—	2	12·7
Swartkrans	—	—	—	—	1	14·2	—	—	2	14·0–14·2
Kaiso	—	—	—	—	—	—	—	—	1	13·3
M^3 Post. Breadth										
T. gelada	9	9·6	8·8–10·3	0·193	1	8·0	—	—	10	8·0–10·3
Kanjera	1	12·8	—	—	3	10·9	10·4–11·2	0·137	6	10·4–12·8
Olorgesailie	—	—	—	—	—	—	—	—	8	13·8–15·9
Makapan	—	—	—	—	—	—	—	—	2	10·2–12·2
Swartkrans	—	—	—	—	1	12·3	—		2	12·2–12·3
Kaiso	—	—	—	—	—	—	—	—	1	11·3
M^3 Length										
T. gelada	9	13·2	11·9–14·0	0·490	1	11·5	—	—	10	11·5–14·0
Kanjera	1	18·1	—	—	3	15·8	14·6–16·6	0·744	6	14·6–18·1
Olorgesailie	—	—	—	—	—	—	—	—	8	18·6–22·5
Makapan	—	—	—	—	—	—	—	—	2	16·9–19·1
Swartkrans	—	—	—	—	1	17·6	—	—	2	16·6–17·6
Kaiso	—	—	—	—	—	—	—	—	1	17·3
M^3 EUL										
Kanjera	1	18·1	—	—	3	16·1	15·2–16·8	0·446	6	15·2–18·1
Olorgesailie	—	—	—	—	—	—	—	—	8	19·0–23·0
Kaiso	—	—	—	—	—	—	—	—	1	17·3
P_3 Breadth										
T. gelada	9	5·1	4·6– 5·4	0·063	1	4·0	—	—		
Kanjera	2	7·05	6·8– 7·3	—	4	6·35	5·9– 6·8	0·103	(All sexed)	
Olorgesailie	5	8·1	7·5– 8·6	0·246	6	6·65	6·2– 7·4	0·166	,,	
Makapan	2	7·0	7·0	—	—	—	—	—	,,	
Swartkrans	2	7·2	6·6– 7·8	0·36	2	5·8	5·6– 6·0	—	,,	
P_3 Length										
T. gelada	9	18·7	17·1–20·4	0·927	1	8·9	—	—	(All sexed)	
Kanjera	1	20·3	—	—	4	12·4	11·4–13·8	2·063	,,	
Olorgesailie	5	19·9	18·3–20·7	0·780	6	12·8	12·0–14·0	0·49	,,	
Makapan	2	24·2	23·4–25·0	0·64	—	—	—	—	,,	
Swartkrans	1	25·1	—	—	2	11·05	10·8–11·3	—	,,	

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
P_3 *EUL*	As Length									
P_4 *Breadth*										
T. gelada	9	6·5	6·0– 7·3	0·119	1	5·9	—	—	10	5·9– 7·3
Kanjera	—	—	—	—	2	7·9	7·8– 8·0	—	3	7·3– 8·0
Olorgesailie	2	9·5	8·8–10·2	—	1	9·6	—	—	10	8·6– 9·7
Makapan	2	8·75	8·5– 9·0	—	—	—	—	—	4	7·1– 9·0
Swartkrans	2	9·25	8·5–10·0	—	2	8·1	7·8– 8·4	—	5	7·8–10·0
Hopefield	—	—	—	—	—	—	—	—	1	9·9
P_4 *Length*										
T. gelada	9	7·5	6·7– 7·9	0·164	1	6·6	—	—	10	6·6
Kanjera	—	—	—	—	2	8·95	8·7– 9·2	—	3	8·7– 9·4
Olorgesailie	2	11·0	10·0–12·0	—	1	10·0	—	—	10	10·0–12·0
Makapan	2	9·5	9·0–10·0	—	—	—	—	—	4	8·2–10·4
Swartkrans	2	11·4	10·8–12·0	—	2	9·15	9·4– 9·5	—	5	9·4–12·0
Hopefield	—	—	—	—	—	—	—	—	1	(11·1)
P_4 *EUL*										
Kanjera	—	—	—	—	2	9·4	9·2– 9·6	—	3	9·2– 9·6
Olorgesailie	2	11·0	10·0–12·0	—	1	10·0	—	—	10	10·0–12.0
M_1 *Ant. Breadth*										
T. gelada	9	7·5	7·2–7·9	0·156	1	6·7	—	—	10	6·7– 7·9
Kanjera	—	—	—	—	3	9·2	8·8– 9·9	0·291	5	8·8– 9·9
Olorgesailie	—	—	—	—	1	11·5	—	—	12	10·5–12·6
Makapan	1	9·5	—	—	—	—	—	—	1	9·5
Swartkrans	1	11·8	—	—	2	10·3	10·1–10·5	—	4	9·8–11·8
Hopefield	—	—	—	—	—	—	—	—	1	9·7
M_1 *Post. Breadth*										
T. gelada	8	7·7	7·2– 8·2	0·075	1	7·1	—	—	9	7·1– 8·2
Kanjera	—	—	—	—	3	9·3	9·0– 9·9	0·200	5	8·6– 9·9
Olorgesailie	1	12·9	—	—	1	10·5	—	—	12	
Makapan	1	9·6	—	—	1	9·0	—	—	2	9·0—9·6
Swartkrans	1	12·3	—	—	2	11·3	11·2–11·4	—	4	10·0–12·3
Hopefield	—	—	—	—	—	—	—	—	1	9·9
M_1 *Length*										
T. gelada	9	10·1	9·5–10·5	0·287	1	9·3	—	—	10	9·3–10·5
Kanjera	—	—	—	—	3	11·2	10·1–12·9	1·544	5	10·1–12·9
Olorgesailie	—	—	—	—	1	14·4	—	—	12	14·4–16·5
Makapan	1	11·8	—	—	1	9·6	—	—	2	9·6–11·8
Swartkrans	1	15·8	—	—	2	11·75	11·3–12·2	—	4	11·3–15·8
Hopefield	—	—	—	—	—	—	—	—	1	(13·8)

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M_1 *EUL*										
Kanjera	—	—	—	—	3	12·9	12·8–13·2	0·044	5	11·9–14·0
Olorgesailie	—	—	—	—	1	15·5	—	—	12	15·5–17·0
M_2 *Ant. Breadth*										
T. gelada	9	9·3	8·8–10·0	0·117	1	8·1	—	—	10	8·1–10·0
Kanjera	—	—	—	—	3	11·6	11·5–11·8	0·02	5	11·5–12·5
Olorgesailie	1	16·0	—	—	1	12·8	—	—	8	12·8–16·0
Makapan	1	12·3	—	—	1	11·2	—	—	2	11·2–12·3
Swartkrans	2	13·2	12·3–14·1	—	2	12·75	12·7–12·8	—	6	12·2–14·1
Hopefield	—	—	—	—	—	—	—	—	1	14·0
M_2 *Post. Breadth*										
T. gelada	9	8·9	8·0– 9·5	0·252	1	8·1	—	—	10	8·0– 9·5
Kanjera	—	—	—	—	3	11·2	11·1–11·3	0·006	5	11·1–11·5
Olorgesailie	1	15·0	—	—	1	13·3	—	—	8	12·4–15·0
Makapan	1	12·1	—	—	1	11·2	—	—	2	11·2–12·1
Swartkrans	2	12·9	12·0–13·8	—	2	12·45	12·4–12·5	—	6	11·7–13·8
Hopefield	—	—	—	—	—	—	—	—	1	15·0
M_2 *Length*										
T. gelada	9	12·7	11·9–13·5	0·185	1	11·1	—	—	10	11·1–13·5
Kanjera	—	—	—	—	3	14·9	13·8–15·5	0·595	5	13·8–15·5
Olorgesailie	1	22·5	—	—	1	17·2	—	—	8	17·2–22·5
Makapan	1	15·9	—	—	1	13·1	—	—	2	13·1–15·9
Swartkrans	2	18·7	17·1–20·3	—	2	15·5	15·4–15·6	—	6	14·8–17·3
Hopefield	—	—	—	—	—	—	—	—	1	16·5
M_2 *EUL*										
Kanjera	—	—	—	—	3	15·6	15·5–15·6	0·023	5	15·5–15·9
Olorgesailie	1	22·25	—	—	1	18·2	—	—	8	17·2–22·5
M_3 *Ant. Breadth*										
T. gelada	8	9·95	9·2–10·7	0·227	1	8·5	—	—	9	8·5–10·7
Kanjera	—	—	—	—	1	12·1	—	—	6	11·7–13·5
Olorgesailie	—	—	—	—	1	15·9	—	—	8	15·1–17·2
Makapan	1	13·2	—	—	1	12·1	—	—	2	12·1–13·2
Swartkrans	1	14·7	—	—	2	13·6	13·4–13·8	—	5	13·1–16·5
Hopefield	—	—	—	—	—	—	—	—	1	18·0
M_3 *Post. Breadth*										
T. gelada	8	9·1	8·2– 9·5	0·205	1	8·0	—	—	9	8·0– 9·5
Kanjera	—	—	—	—	1	11·3	—	—	6	11·3–12·0
Olorgesailie	—	—	—	—	1	14·5	—	—	8	13·2–15·6
Makapan	1	12·1	—	—	1	10·8	—	—	2	10·8–12·1
Swartkrans	1	13·3	—	—	2	12·45	12·0–12·9	—	5	12·0–15·2
Hopefield	—	—	—	—	—	—	—	—	1	16·5

Table 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M_3 *Length*										
T. gelada	8	16·6	16·0–17·2	0·194	1	14·0	—	—	9	14·0–17·2
Kanjera	—	—	—	—	1	20·0	—	—	6	19·8–23·2
Olorgesailie	—	—	—	—	1	24·7	—	—	8	23·7–27·3
Makapan	1	21·0	—	—	1	18·9	—	—	2	18·9–21·0
Swartkrans	1	26·5	—	—	2	21·4	20·1–22·7	—	5	20·1–26·5
Hopefield	—	—	—	—	—	—	—	—	1	26·8
M_3 *EUL*										
Kanjera	—	—	—	—	1	20·1	—	—	6	20·0–23·5
Olorgesailie	—	—	—	—	1	24·7	—	—	8	23·7–27·3

Cheek-tooth dimensions in Olduvai *Simopithecus*

No.	Site/Bed	Sex	Tooth	Ant. Br.	Post. Br.	Length	EUL
301	BK II	?	M^1	13·8	12·7	15·2	15·8
262	SHK II	?	M^1	12·4	(12·9)	13·2	(15·1)
622	SHK II	?	M^1	13·1	(12·5)	12·1	(14·7)
M 14939	II	?	M^2	16·2	15·0	20·9	21·0
1091	BK II	?	M^2	14·6	14·1	19·0	19·4
M 14681	?	?	M^2	14·4	13·9	16·3	17·0
,,	?	?	M^3	14·0	12·4	18·0	19·0
1096	BK II	?	M^3	17·1	14·5	22·5	23·0
436	BK II	?	M^3	16·8	13·7	21·3	21·3
M 14953	II	F	M_1	11·8	10·7	11·0	12·2
,,	,,	,,	M_2	13·3	12·8	17·1	17·5
,,	,,	,,	M_3	14·4	13·0	24·1	24·1
M 14937	DKI	?	M_1	9·0	9·8	10·3	(12·0)
,,	,,	?	M_2	11·8	11·3	14·5	15·4
,,	,,	?	M_3	13·5	12·3	20·2	20·5
Juv. (no no.)	BK II	F	M_1	11·0	11·4	14·5	14·7
,,	,,	,,	M_2	12·6	12·4	17·8	18·1
Ex. 117	,,	?	M_2	13·7	12·6	16·6	17·6
200	BK II	?	M_2	13·7	13·1	19·1	19·2
694	GRC	?	M_2	14·2	13·7	18·4	18·5
1332	GRC	?	M_3	14·3	13·6	24·9	25·1
'Olduvai'	?	?	M_3	14·7	12·7	23·5	23·9
M 14938	DKI	F	M_3	14·7	12·6	21·9	22·2
M 14680	IV	M	M_1	12·0	12·0	16·4	16·4
,,	,,	,,	M_2	16·2	15·1	21·1	21·1
580, 57	JLK IV	F	M_1	11·3	11·1	13·6	15·5
,,	,,	,,	M_2	15·7	13·6	17·0	18·9
,,	,,	,,	M_3	16·6	14·0	23·8	24·0

TABLE 4 (continued)

No.	Site/Bed	Sex	Tooth	Breadth	Length	EUL
M 18779	II	F	P^3	10·1	8·2	8·2
,,	,,	,,	P^4	11·4	9·9	9·9
M 14938	DKI	F	P_3	5·8	13·0	13·3
,,	,,	,,	P_4	7·4	10·6	10·8
Juv.	BK II	F	P_3	7·1	13·4	13·4
,,	,,	,,	P_4	8·5	10·5	10·5
M 14680	IV	M	P_3	9·4	17·7	17·7
,,	,,	,,	P_4	11·2	12·8	12·8
580,57	JLK IV	F	P_3	(8·5)	(12·0)	?
,,	,,	,,	P_4	10·5	11·5	(12·0)

Forelimb

The *scapula* is represented by four fragmentary specimens, all undescribed and unregistered (Plate 11a and b):

1. A fragment of a left acromion, excluding the extreme tip.
2. A fragment of the distal end of a right scapula, including the posterior part of the glenoid cavity, a short length of the anterior border, and the acromion.
3. A larger fragment consisting of the glenoid region, part of the cranial and axillary margins, the base of the acromion, and the adjoining part of the spine, of which the free edge is absent.
4. An isolated left glenoid region, with a small portion of the neck and the axillary border.

The dimensions of the specimens are shown in Table 5. The areas of origin of the

TABLE 5

Dimensions of scapula in *Simopithecus* and representative specimens of extant species

Dimensions: a. Breadth across acromion and glenoid fossa
b. Breadth of glenoid articular surface
c. Height of glenoid articular surface.

Site/Species and Specimen No.	No. in descriptive list	Known or probable sex	Dimensions a.	b.	c.
Kanjera	2	?	47·5	22·5	
	3	?	—	22·5	30
	4	?	—	23·5	33
Olorgesailie		?	—	(29)	(35)
		?	—	(29·5)	(41)
		?	—	27	39
T. gelada AMNH 60568	–	M	40	17	23
U. primatol.	–	M	41	17	22
P. anubis AMNH 82097	–	M	46	19	27
AMNH 82096	–	F	37	16	24·5
Pan USNM 176230	–	M	49	24	31
USNM 176227	–	F	45	23	28
Gorilla USNM 239883	–	M	78	40	56
USNM 220060	–	F	53	29	35

spino- and acromio-deltoid muscles agree with the condition in living genera. The acromion itself is rather short and stout, and also oriented as in the terrestrial rather than the arboreal modern genera. The neck is rather broad, indicating a stout and heavy build. The areas of origin of the round and aponeurotic portions of M. triceps, caput longum, are strongly-marked. The spino-glenoid notch is deep.

The *humerus* is represented by eleven specimens, of which seven are new, and which between them represent the whole bone (Plate 11c, d and e):

1. Part of the proximal end of a right humerus, from the surgical neck to the level of the midpoint of the delto-pectoral crest. An isolated head with part of the lesser tuberosity makes a good fit with the posterior part of its broken proximal surface.
2. Part of the shaft of a left humerus, showing the anterior surface in the region of the deltoid insertion.
3. M 18791. Part of a left humeral shaft, from just above the midpoint of the insertion of M. teres major to well below the delto-pectoral crest.
4. A fragment of a left shaft, almost exactly as the last, but less complete distally.

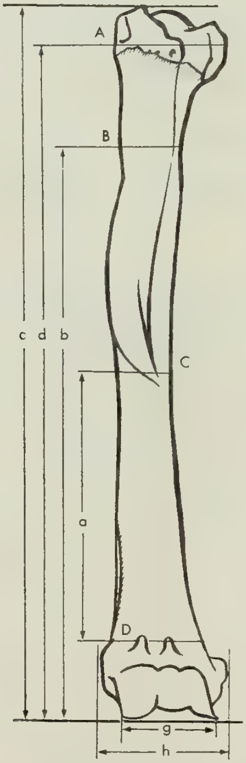


FIG. 4. Anterior aspect of humerus, showing dimensions quoted in Table 6. A. Horizontal plane at most proximal point of diaphysis. B. Plane at midpoint of insertion of M. teres major tendon. C. Plane where deltoid crest crosses anterior margin. D. Plane immediately proximal to tubercle of insertion of M. extensor radialis longus.

5. The distal part of a right shaft, with the distal end of the deltoid insertion, broken distally just proximal to the anconeal fossa.

6. Fragment of the distal end of a humeral shaft, broken distally as No. 5, proximally just above the upper end of the brachioradialis crest.

7. Fragment resembling No. 5, but with less preserved both proximally and distally.

8. M 11542. Fragment of a left humerus, well-preserved distal to the level of the insertion of M. teres major, but with most of the deltopectoral crest and the radial epicondyle broken away.

9. M 18789. The complete distal extremity of a right humerus.

10. M 11543. The distal part of a left humerus, much as No. 8, but more complete anteriorly.

11. M 18721. The distal part of a left humerus, the posterior surface preserved from above the level of the distal end of the deltoid insertion, the anterior surface broken in this region, but preserved distally.

Dimensions are shown in Table 6.

In none of the specimens is the greater tuberosity preserved, so that its projection beyond the level of the head, an indication of terrestrial adaptation (Jolly, 1967) cannot be determined. The head itself (one specimen) appears to be rather flatter, less hemispherical, than in any of the living Cercopithecoidea, but this feature is not easy to measure objectively. In all the nine specimens in which the region is preserved, the area of origin of M. brachialis extends broadly on to the posterior surface, thus agreeing with all the modern Cercopithecinae examined except the single specimen of *Theropithecus gelada* dissected. This can be deduced from the position of the raised line dividing the area of origin of the brachialis from that of triceps, and from the presence of a distinct line running between the prominent deltoid-triceps-brachialis crest and the large triceps lateralis rugosity on the lateral aspect of the proximal end.

The region of the lateral epicondylar ridge is preserved wholly or partly in seven specimens. In none is it raised prominently above the profile of the lateral margin of the humerus, as it is in the large climbing forms *Macaca* and *Mandrillus*, which have powerful Mm. brachialis and brachioradialis.

The third reliable indicator of terrestrial adaptation, the relative breadth of the distal articular surface expresses the relative size of the epicondyles, especially the ulnar, which is large and prominent in arboreal monkeys (Jolly, 1967).

The dimensions of overall distal breadth and articular breadth of three Kanjera specimens are plotted in Fig. 5 together with those of the modern series. With indices (100 × articular breadth/bi-epicondylar breadth) of 70·8, 71·7 and 75·0, these lie beyond the range of the arboreal series, and with the modern baboons.

Judging by size Nos 1, 4, 6, 8, 9 are from male individuals, 3, 5, 10, 11 from females. Nos 1 and 9 are possibly parts of the same humerus, while 8 is closely similar in size, and may well be its pair. The midpoint of the insertion of M. teres major occurs on both 1 and 8, enabling the approximate overall length of the male humerus to be estimated (236 mm). The unbroken length of No. 8 can be estimated from the

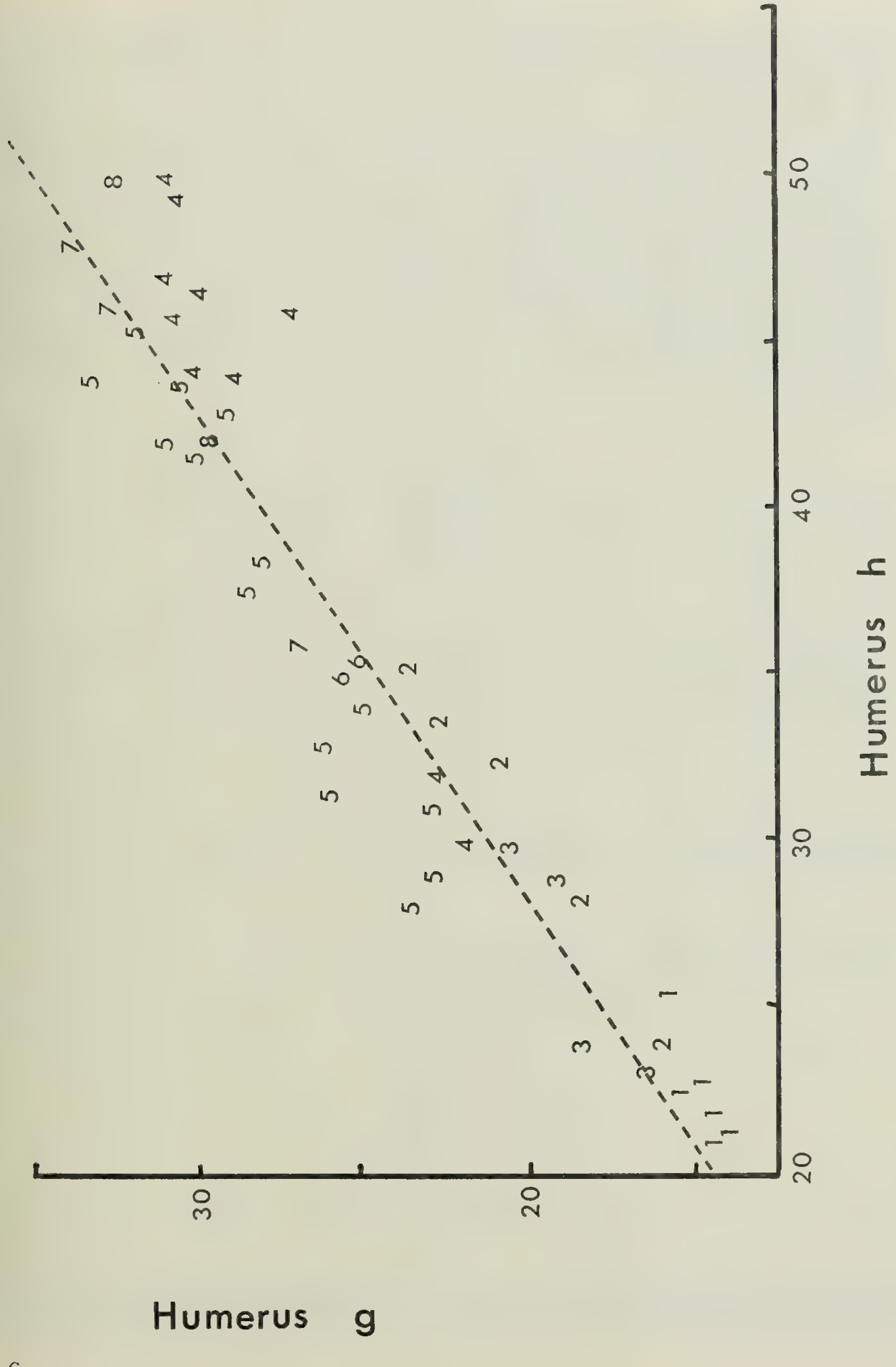
Table 6

Dimensions of humerus in *Simopithecus* and representative specimens of extant species
For Dimensions a–d see Fig. 4.

e. Transverse diameter at B (Fig. 4)
f. Transverse diameter at D (Fig. 4)
g. Breadth of distal articular surface
h. Bi-epicondylar breadth
i. Antero-posterior diameter at B (Fig. 4)
j. Antero-posterior diameter at C (Fig. 4)
k. Minimum antero-posterior diameter of trochlear surface.

Site/Species and Specimen No.	No. in Descriptive list	Known or Probable Sex	Dimensions (see Fig. 4) a.	b.	c.	d.	e.	f.	g.	h.	i.	j.	k.
Kanjera	1	(M)	—	—	—	—	20	—	—	—	25·5	—	—
M 18791	3	(F)	—	—	—	—	16	—	—	—	19·5	18	—
—	4	(M)	—	—	—	—	19·5	—	—	—	23	22	—
—	5	(F)	80	—	—	—	—	24·5	—	—	—	17	—
—	6	(M)	—	—	—	—	—	32	—	—	—	—	—
M 11542	8	(M)	92	178·5	—	—	20	33	34	48	—	22·5	17
M 18789	9	(M)	—	—	—	—	—	34	33	46	—	—	17
M 11543	10	(F)	66	140·5	—	—	14·5	29	27	36	19	16	14
M 18721	11	(F)	—	—	—	—	—	29	26	—	—	—	13·5
Olorgesailie													
2993	1	(M)	100	226	—	267	23	46	44	62	28	28	(20)
FU1/UL	4	?	—	—	—	—	—	—	(34)	—	—	—	17
FU2/UL	5	(F)	—	—	—	—	—	—	(36·5)	—	—	—	20
FU3/UL	6	(?F)	—	—	—	—	—	—	36	—	—	—	18
Olduvai													
1384 BK II E	1	?	104·5	—	—	—	—	37·5	29·5	42	–	22·5	14
BK II 118	2	?	91	(172)	—	—	—	32	—	—	—	18	16
SWK F2953	3	?	—	—	—	—	—	—	32·5	50	—	—	16
T. gelada													
U. Primatol.	—	M	79·5	148	194	—	15	25	22·5	36·5	17	17	14
AMNH 60568	—	M	87	161	204	193	17·5	25	25	36	17	16·5	13
P. anubis													
AMNH 82097	—	M	98	189	245	234	16	35	30	45	19	21	15
AMNH 82096	—	F	83·5	156	206	199	15	29	26	34·5	18	18	14
Pan													
USNM 176230	—	M	116	254	325	304	25	50	46	64	22	23	19
USNM 176227	—	F	108	201	283	264	22	43	42	58	22	22	15
Gorilla													
USNM 239883	—	M	128	302	424	—	39	84	72	106	40	36	23
USNM 220060	—	F	125	258	360	—	24	50	49	69	24	23	18

Fig. 5. Proportions of the distal end of the humerus in Cercopithecinae. Dimensions as shown in Fig. 4. 1. *Cercopithecus*. 2. *Macaca*. 3. *Cercocebus*. 4. *Mandrillus*. 5. *Papio*. 6. *T. gelada*. 7. *Simopithecus* (Kanjera). 8. *Simopithecus* (Olduvai).



c

value of the expression: overall length/length midpoint M. teres major insertion to capitulum, obtained from a *Theropithecus gelada* humerus. This gives a closely similar value, 233 mm.

The same formula may be used to calculate the unbroken length of the small female specimen (10). A value of 184 mm is obtained using gelada proportions, 186 mm using the reconstructed length of the male humerus. However, No. 10 is consistently the smallest specimen of the female series. Anterior-posterior breadth at the distal end of the deltoid crest averages 17 mm and ranges up to 18 mm. in the limited female sample. If length varied in proportion, it would have been about 196 mm in an average, and 209 mm in a large female.

All six specimens of the *radius* are registered in the British Museum collection (Plate 12d and e).

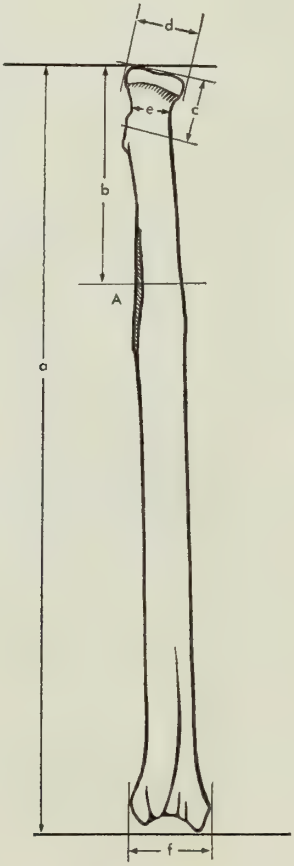


FIG. 6. Posterior aspect of radius, showing dimensions quoted in Table 7. A. Horizontal plane bisecting area of attachment of strong, oblique part of interosseous ligament.

1. M 11544. A left radius, with all the surface details well-preserved, complete apart from some slight erosion of the head. The details of the surface resemble those seen in *Theropithecus gelada* rather closely, but the muscular moulding of the shaft is stronger and the interosseous border rather more prominent. The area corresponding to the attachment of the strong, oblique part of the interosseous membrane is distinguishable, and a small, roughened area on the volar surface, immediately distal to the bicipital tuberosity, probably represents the origin of the M. abductor pollicis longus. The crest separating the positions of the extensors and abductor pollicis longus in the distal third of the shaft is prominent, but rounded, as in *Theropithecus gelada,* without the lipping frequently present in more arboreal monkeys. The shaft has slight posterior convexity, and rather greater lateral convexity than is seen in *Theropithecus gelada* and the more gracile forms of *Papio,* resembling the more heavily built forms of *Papio,* and *Mandrillus.* The morphology of the distal extremity resembles that of *Theropithecus gelada.* From its size, the specimen probably represents a female individual.

2–6. The remaining specimens of the radius, which are heads with variable amounts of shaft preserved (M 18801, 18802, 18717, 18716, 11545) agree in structure with M 11544, especially in the deep excavation of the volar surface and the prominence of the interosseous border. Their dimensions are shown in Table 7.

The size of the specimens, so far as this can be gauged from the breadth of the head and neck, indicates that 2, 3 and 5 are from males, and 1, 4 and 6 from females. The overall length of No. 1 is 198 mm. This was evidently from a large female; the mean of neck breadth in the female series is 12·3 mm, and the lowest value 12·0 mm (94·6 and 92·3%, respectively, of the neck breadth of No. 1). If their length was proportionately less than that of No. 1, this would have been about 187 mm in an average, and 183 mm in a small female.

The unbroken length of the male fragment No. 2 can be estimated from the proportions of the whole female radius (No. 1) by using the formula: total length/length from head of midpoint of insertion of the strong, oblique part of the interosseous membrane.

This gives a value of 224 mm for No. 2, the largest of the male fragments. Adjusting this value with reference to neck breadth allows an estimate of 216 mm for radius length in average-sized males, and 208 mm in small ones.

Eight specimens of the *ulna* are present in the Kanjera collection, of which one is unregistered (Plate 12a–c).

1. M 11546. Complete apart from the distal epiphysis.

2. A fragment of shaft (unregistered).

3–8. M 18722, 18723, 18724, 18725, 18726, 18803. Proximal ends with a variable amount of shaft attached.

In all the specimens, the interosseous line is prominent. The details of morphology of the proximal end are somewhat variable, especially the degree of excavation of the medial surface. In all the specimens, the articular surface of the anconeal

TABLE 7

Dimensions of radius in *Simopithecus* and representative specimens of extant species

a. Radial length
b. As in Fig. 6
c. Distance from head to midpoint of bicipital tuberosity, parallel to axis of neck
d. Maximum diameter of radial head
e. Minimum value of greatest diameter of radial neck
f. Maximum breadth, distal end.

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions					
			a.	b.	c.	d.	e.	f.
Kanjera								
M 11544	1	(F)	198	79	24·5	16·5	12·5	23
M 18801	2	(M)	—	88·5	29	22·5	15	—
M 18802	3	(M)	—	—	29	22	14·5	—
M 18717	4	(F)	—	—	20·5	17	12	—
M 18716	5	(M)	—	—	25·5	20·5	14	—
M 11545	6	(F)	—	—	19	17	12	—
Olorgesailie		?	—	—	—	21·5	—	—
OG–1463		?	—	—	—	—	—	30
OG–1462		?	—	—	—	—	—	—
Olduvai								
IS 1941	1	(?F)	—	—	25	21·5	16	—
BK II 1953/4	2	(?M)	—	—	36	25	17·5	—
Hopefield	—	?	—	—	—	19	—	—
T. gelada								
U. Primat.	—	M	210	63	19	17	12	22
AMNH 60568	—	M	220	63	19	17	12	19
P. anubis								
AMNH 82097	—	M	243	65	28	20	14	27
AMNH 82096	—	F	210	55·5	23·5	17·5	12	22·5
Pan								
USNM 176230	—	M	305	—	40	27	14	33
USNM 176227	—	F	266	—	40	22	14	34
Gorilla								
USNM 239883	—	M	364	126	68	36	19	57
USNM 220060	—	F	285	94	52	95	15	38

process faces markedly more laterally and distally than medially; in extreme specimens such as M 18723 no medially-facing part is present. The markings representing the attachments of the M. brachialis and of the humero-ulnar ligament are clearly visible in all specimens in which the coronoid process is preserved. In the unregistered shaft fragment three longitudinal raised lines are present, probably representing the interosseous line, the ridge from which the M. extensor pollicis longus and extensors of the second and third digits originate, and the fascial line dividing the latter muscle-group from the M. extensor carpi ulnaris.

In all eight specimens in which the olecranon is preserved, it is massive and obviously backwardly-reflexed in the manner typical of *Papio* and *Theropithecus gelada*. In three specimens (M 18724, M 18726, M 11564) sufficient of the shaft is preserved to permit determination of the olecranon/shaft angle (Jolly, 1967). The values obtained (60°, 73°, 50°) lie well above the upper limit for all modern genera apart from

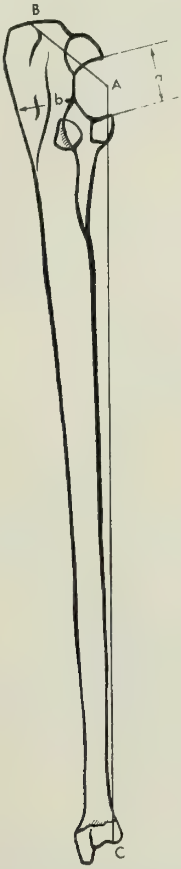


FIG. 7. Lateral aspect of ulna, showing dimensions quoted in Table 8. A. Centre of rotation of humeral articulation. B. Centre of rotation of ulnar head.

TABLE 8

Dimensions of the ulna in *Simopithecus* and representative specimens of extant species

a. Distance from tip of coronoid process to tip of anconeal process
b. Minimum antero-posterior diameter in humeral articulation
c. Distance along AC from A to distal epiphyseal line (Fig. 7)
d. Length AC (Fig. 7).

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions			
			a.	b.	c.	d.
Kanjera						
M 11546	1	(F)	18·5	19	222·5	—
M 18722	3	?	—	19	—	—
M 18723	4	(M)	21·5	19	—	—
M 18724	5	(F)	18	16·5	—	—
M 18726	7	(M)	20	21	—	—
M 18803	8	?	17	15·5	—	—
Olorgesailie	—	?	26	—	—	—
T. gelada						
U. Primat.	—	M	17	14·5	205	209
AMNH 60568	—	M	16·5	14·5	214	220
Papio anubis						
AMNH 82097	—	M	21	17	232	237
AMNH 82096	—	F	16·5	16	214·5	217
Pan						
USNM 176230	—	M	24	21	289	297
USNM 176227	—	F	20	20	252	259
Gorilla						
USNM 239883	—	M	27	34	329	349
USNM 220060	—	F	22	23	265	272

the baboons, and at the upper end of the range of these (Fig. 8). None of the specimens show the antero-posterior broadening of the shaft posterior to the humeral articulation, which is distinctive of *Mandrillus* and some specimens of the larger species of *Macaca.*

The ulnar fragments do not fall clearly into two differently-sized groups, although the massive fragments Nos 4 and 7 can safely be attributed to males, and No. 5, which is much smaller, though mature, to a female. No. 8 is small but has an unfused acromial ephiphysis. No. 1 was from an almost mature individual, since only the distal epiphysis was unfused.

Hindlimb and Axial Skeleton

The *sacrum* is represented by a single specimen (M 18715) consisting of the two proximal sacral vertebrae, with the wings somewhat damaged and the superior articular processes absent. The articular crest of both sides has been sheared off, exposing the ventral floor of the neural canal. The distal surface is smooth and articular anteriorly, but posteriorly is broken away, indicating that an incompletely fused third sacral vertebra was present, as is regularly found in large Cercopithecoidea.

The *pelvis* is represented by eight specimens (M 11547, 18711, 18712, 18713, 18714, 18792, 18804, and an unregistered fragment). Between them they include the whole innominate bone, apart from the ischial tuberosities, the crest of the ilium, and part of the pubic ramus. The pelvis of *Simopithecus* was evidently similar in shape and proportions to that of other large Cercopithecoidea.

In spite of the difference in orientation of the tail in the living animal, no consistent distinction could be demonstrated in the tilt of the sacrum on the ilium between *Papio* and *Mandrillus* and *Theropithecus gelada.*

The *femur* is represented by eight fragments, of which three are unregistered (Plate 13a–c).

1. M 18807. Head, neck and adjoining part of the shaft of a right femur.
2. M 18710. Fragment from the proximal end of a right femur, with the lesser trochanter, but without the greater trochanter, head and neck.

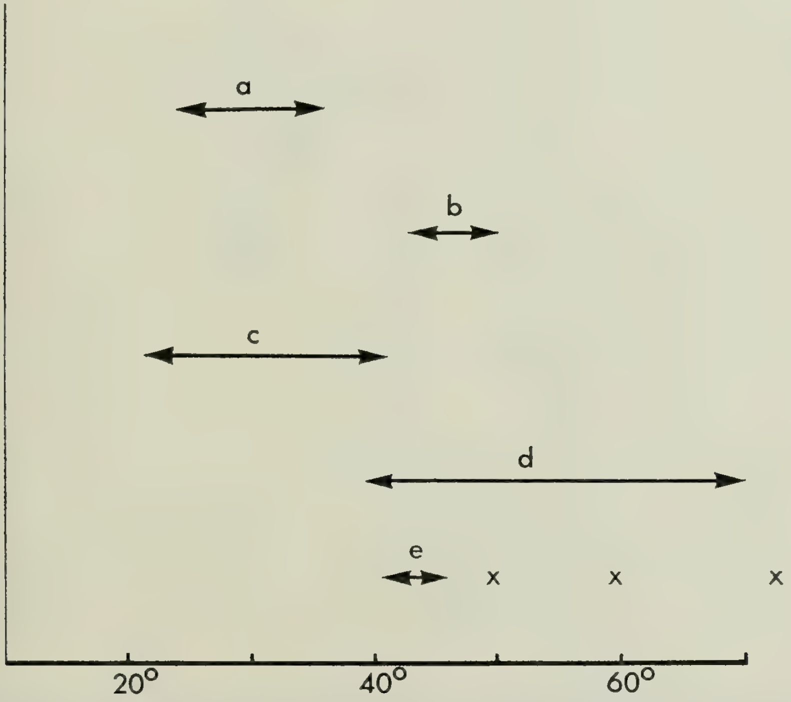


FIG. 8. Range of olecranon inclination angle in cercopithecine ulnae. Crosses represent Kanjera *Simopithecus* specimens. a. *Macaca* (N = 15). b. *Mandrillus* (N = 3). c. *Cercocebus* (N = 5). d. *Papio* (N = 24). e. *T. gelada* (N = 2).

3. M 18709. Fragment from the proximal end of a right femur, broken transversely at the level of the lesser trochanter.

4. M 11548. The greater part of a left femur, broken proximally at about midway along the intertrochanteric crest, distally at the level of the shallow pit representing the position of the bursa lying beneath the quadriceps tendon.

5. M 18708. Part of a right femur, almost exactly as the last, but with rather less of the proximal end preserved.

6. Fragment of the distal end of the shaft of a right femur, with the anterior surface somewhat damaged.

7. Part of the proximal end of a right femoral shaft, with part of the lesser trochanter.

8. A fragment from the proximal end of a left femoral shaft.

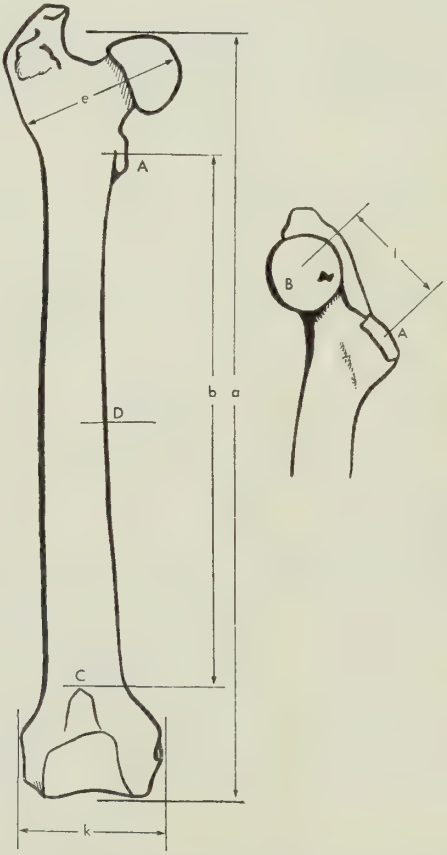


FIG. 9. Anterior aspect of femur, showing dimensions quoted in Table 9. A. Midpoint of surface of lesser trochanter. B. Midpoint of head of femur. C. Transverse plane at proximal margin of shallow pit lying beneath quadriceps tendon. D. Transverse plane midway between A and C.

Dimensions are shown in Table 9. All but the distal extremity and the tip of the greater trochanter is present in one or more of the specimens.

TABLE 9

Dimensions of femur in *Simopithecus* and representative specimens of extant species

a., b., e. See Fig. 9

c. Maximum diameter of femoral head
d. Maximum diameter of femoral neck
f. Maximum diameter of shaft through lesser trochanter
g. Transverse diameter at D (Fig. 9)
h. Antero-posterior diameter at D (Fig. 9)
i. Transverse diameter at C (Fig. 9)

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions (see Fig. 9)								
			a.	b.	c.	d.	e.	f.	g.	h.	i.
Kanjera											
M 18807	1	(M)	—	—	27	22	53	—	—	—	—
M 18710	2	(F)	—	—	—	—	—	29·5	—	—	—
M 18909	3	(M)	—	—	—	33·5	—	—	—	—	—
M 11548	4	(F)	—	134·5	—	—	—	29·5	15·5	16	22
M 18708	5	(F)	—	135	—	—	—	30	16·5	18	22
	6	(M)	—	—	—	—	—	—	21*	18*	—
	7	(F)	—	—	—	—	—	30	—	—	—
Olorgesailie											
MS 3991	1	(F)	232	—	—	19	61	—	20	23	—
1731	2	(M)	—	—	35	26	78	—	26	29	—
	3	(M)	—	—	33·5	26·5	77	40·5	—	—	—
	4	(M)	—	—	—	—	—	45	—	—	—
	6	(M)	—	—	—	—	—	(39)	—	—	—
Olduvai											
BK II 693	1	?	—	—	28	21	56·5	30	—	—	—
SHK II E 1203	2	?	—	—	29	25	58·5	—	—	—	—
BK II E 1383	3	?	—	—	—	—	—	—	—	—	28
	4	?	—	—	—	—	—	—	—	—	28·5
T. gelada											
U. Primatol.	—	M	209	140	21	14	44	27	15·5	16	19·5
AMNH 60568	—	M	214	145	21	15	43	27·5	15	14·5	19
P. anubis											
AMNH 82097	—	M	259	183	25	18	54	29	16·5	18	22
AMNH 82096	—	F	232	164	22·5	16	45	24	15	16	21·5
Pan											
USNM 176230	—	M	327	232	37	27	77	40	25	23	36
USNM 176227	—	F	284	194	31	20	67	34	23	21	28
Gorilla											
USNM 239883	—	M	385	240	54	39	110	63	43	36	65
USNM 220060	—	F	299	196	36	23	80	37	27	23	39

* Correct position estimated

The neck is rather short and broad, resembling the condition in *Mandrillus* and *Papio* rather than *Theropithecus gelada*, but the feature is variable. The shaft shows rather strong anterior convexity in all specimens, resembling *Theropithecus* rather than the other living Cercopithecinae, and the muscular impressions, especially the branch of the linea aspera upon which the adductor musculature inserts, are strong.

From their size, Nos 1, 3 and 6 are from male individuals, 2, 4 and 5 from females. The unbroken length of the female femur can be estimated from the two almost complete shafts, Nos 4 and 5, using the formula: overall length/length from mid-point of lesser trochanter to level of proximal margin of sub-quadriceps pit, and substituting the value obtained on the gelada femur. The unbroken lengths of Nos 4 and 5, estimated in this way, are both 201 mm.

The length of the male specimens cannot be directly estimated. However, the breadth through the lesser trochanter of male No. 3 is 112·6% of the mean of female values for this dimension; if its length when unbroken was proportional to this, it was about 226 mm. Fragments Nos 1 and 6 probably came from slightly larger animals; estimates of their unbroken lengths (assuming that their breadth dimensions preserved the same ratios one to another as observed in *Theropithecus*, and that the ratio of length to breadth dimensions was as in female *Simopithecus*), are 234 mm and 231 mm respectively.

Three fragments of the *tibia* are preserved: two distal extremities (M 18718, M 18719) and part of the proximal end. The latter is unregistered.

The two distal ends show the usual cercopithecine features, including the distinct grooves crossing the posterior surface which in life accommodate the tendons of the long digital flexors and M. tibialis posterior. The pit on the lateral surface, representing the position of the inferior tibio-fibular joint, bounded by the rugose area to which the tibio-fibular ligament was attached, is clearly visible. The fragment of the proximal end shows no remarkable features, apart from a prominent rugosity, running antero-proximally, immediately distal to the supposed epiphyseal surface. If the interpretation of the topography of the fragment is correct, this rugosity is too proximally situated to represent the site of attachment of the medial collateral ligament, and must be regarded as pathological. Dimensions of the tibial fragments are shown in Table 10. None of the fragments is sufficiently large to permit the unbroken length of the bone to be reconstructed.

Both the rather small fragments, representing the distal end of the *fibular* shaft, are unregistered. They show no features to distinguish them from modern Cercopithecinae. In one of them, the area of the attachment of the tibio-fibular ligament on the medial surface, and a small part of the tibio-fibular articular facet, can be distinguished.

The tarsus is represented by an associated *calcaneus*, *talus* and *cuboid* (M 18806, M 11549, M 18805) (Plate 13). The talus and calcaneus show no features to distinguish them from corresponding bones in living Cercopithecoidea of similar size. The cuboid resembles that of *T. gelada* in that its lateral border is markedly shorter than its medial, giving it a wedge-shaped outline from the dorsal aspect.

TABLE 10

Dimensions of tibia in *Simopithecus* and representative specimens of extant species

a. Maximum antero-posterior diameter of distal end
b. Maximum transverse diameter of distal end
c. Ant.-Post. diameter immediately below most distal point of proximal epiphysis
d. Breadth of articular surface of medial condyle, to tip of intercondylar eminence
e. Minimum antero-posterior diameter
f. Maximum length of diaphysis
g. Overall length

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions						
			a.	b.	c.	d.	e.	f.	g.
Kanjera									
M 18718	—	?	21·5	29	—	—	—	—	—
M 18719	—	?	23	—	—	—	—	—	—
Unregistered	—	?	—	—	(32)	—	—	—	—
Olorgesailie		?	—	—	—	—	—	—	—
	1	?	—	—	—	20	—	—	—
	2	?	—	—	—	—	17·5	—	—
3723	4	?	—	—	(33)	—	16·5	135	—
3966	5	?	—	—	—	—	(21)	—	—
2108	6	?	—	31	—	—	—	—	—
T. gelada									
U. Primat.	—	M	19	24·5	23	15·5	13	(189)	214
AM 60568	—	M	19	24	24	16·5	13·5	(188)	218
P. anubis									
AMNH 82097	—	M	22	26·5	—	17	16	—	230
AMNH 82096	—	F	18·5	22	—	15·5	13	—	200·5
Pan									
USNM 176230	—	M	29	41	33	26	18	—	275
USNM 176227	—	F	25	36	28	26	19	—	238
Gorilla									
USNM 239883	—	M	40	65	48	38	26	—	307
USNM 220060	—	F	27	42	33	27	18	—	239

B OLORGESAILIE

The deposits at Olorgesailie, Kenya, were described by Leakey (1946) and by Isaac (1966a and 1966b), who summarized the results of his own and previous research. They consist of a series of volcanic ashes, tuffs and reworked sands and gravels of volcanic origin, laid down in the beds of swamps and sluggish, seasonal streams occupying a basin of tectonic origin. The *Simopithecus* remains were virtually all derived from a presumed Acheulian camp and butchering site, DE 89 (Isaac, 1966b), situated on Land Surface 7 of Leakey (Cole, 1954, p. 144). They represent the remains of human meals.

The *Simopithecus* specimens are less well-preserved than those from Kanjera. The nature of the deposit was evidently less favourable for fossilisation, since the surface of many specimens is eroded and friable, with surface detail hard to distinguish. Most of the long-bones were thoroughly cracked and broken, presumably by humans and scavenging carnivores. In addition, most of the individuals represented here were juvenile, so that many epiphyses have been lost. In other respects the material is excellent, specially in the richness of representation of the smaller bones of the extremities, and the almost mint condition of many of the teeth, not a few of which were unerupted crown-germs.

Skull

Useful skull fragments are comparatively rare in the Olorgesailie collection. All are hitherto undescribed.

a. KNM–OG 1421. A fragment of the right temporal, including the glenoid articular area and the zygomatic root. The fragment resembles the corresponding part of the Kanjera female specimen, M 14936, as far as can be seen, but is larger.

b. KNM–OG 1450. The anterior part of a frontal, with the interorbital region presented, but the supraorbital tori absent. The prominent temporal lines curve strongly towards the midline, and obviously came very close to meeting, or actually met, on the frontal bone itself.

c. KNM–OG 1451, 1452, 1453. Three half-frontals, one right, two left, all broken longitudinally exactly in the midline, suggesting that a line of weakness existed in the immature skull along the line of the metopic suture. In the two specimens where this region is preserved, the coronal suture was evidently open at the time of death. In all cases the temporal lines are strongly curved towards the midline.

d. KNM–OG 0001. Part of a juvenile, male, right maxilla, with the series P^3–M^2; a deep concavity on the broken anterior surface represents the alveolus, or perhaps the crypt of the canine, and enables the sex of the individual to be established. M^1 shows slight-moderate wear, with the central dentine 'bridge' just open; M^2 shows slight wear; P^4 shows slight, and P^3 very slight attrition.

The shape of the specimen, so far as can be seen, resembles that of the Kanjera male specimen. With the occlusal plane horizontal, the root of the zygomatic arch lies over the second molar.

e. KNM–OG 0004. Part of the region of the symphysis and right mandibular corpus of an adult male individual. Almost the entire internal face of the right corpus is preserved; the external face is broken away posterior to the position of the fourth premolar. The broken stump of the right canine, and the two right premolars are present. The region of the symphysis is broken obliquely just to the left of the midline, so that the alveolus of the left canine is opened, and the posterior surfaces of the incisor sockets are visible.

The specimen is rather massive. The inferior surface is flat and triangular in shape, as in the Kanjera *Simopithecus*. The canines are stout, and set obliquely, so that their sockets converge inferiorly. The anterior part of the symphyseal surface, between the canines, is extremely narrow, again as in the Kanjera specimens, implying a reduction in the breadth of the incisor series. On the internal surface of the symphysis the usual two shelves are present; the superior one extends posteriorly to the level of the posterior margin of P_3, the inferior to the level of the intercusp clefts of M_1. No trace of a mandibular fossa is apparent on the part of the external surface that is preserved. Behind the narrow incisal region, the corpora diverge markedly, giving a distinctly V-shaped outline to the jaw when viewed from above.

f. KNM–OG 0002. 'Site 10, Bed B, Tr. Fr.' (Plate 18a).

An almost complete right mandibular corpus of a young adult female, with all the premolars and molars present. The specimen is broken anterior to the premolars, but the alveolus of the canine and a small part of the root of the lateral incisor are preserved. The teeth are somewhat damaged, and the chin region is absent. The symphysis is broken just to the right of the midline, but the profile of the two shelves is visible.

The premolars show only slight wear; there is moderate wear on the first and second molars, while the third is newly erupted and shows very slight wear only on the tips of the anterior pair of cusps. A very shallow mandibular fossa, elongated and situated immediately above the inferior margin of the corpus is present. The superior of the two symphyseal shelves extends posteriorly as far as the middle of the fourth premolar; the inferior to the level of the anterior cusps of the first molar.

g. KNM–OG 0003. Part of the right mandibular corpus of a juvenile male, broken at the symphysis. The surfaces of the specimen are badly eroded. The first and second permanent molars are present, M_1 somewhat damaged at its antero-lingual corners. P_4 had not started to erupt at the time of death, but the germ of the crown, in its crypt, has been exposed by breakage. M_2 is only slightly worn; M_1 shows slight-moderate wear, with the central dentine 'bridge' just open. Little morphological detail is visible, apart from the fact that the surface flares outwards in the region of the root of the canine, thus producing a shallow mandibular fossa posterior to this.

h. KNM–OG 0781. Part of the left corpus mandibulae of a juvenile male, slightly younger than the last at death, extending from the level of the canine to that of M_2. At the time of death, the tip of the canine was just about to penetrate the alveolus; it has been exposed by breakage. P_3, the crown of which has also been exposed by breakage since fossilisation, was also unerupted, lying close behind the canine. P_4 is entirely invisible. M_1 was fully in occlusion at death, and shows light-moderate wear. M_2 had emerged from its bony crypt. The specimen agrees in morphology with the previous one.

i. KNM–OG 0005. A fragment of the left mandibular corpus of a young adult male individual, with P_3–M_1. The surface of the mandible is somewhat eroded, and the inferior border is absent. The first molar shows moderate wear, but both premolars are unworn.

Teeth

The structure of the molars and premolars, which are all well-represented, mostly by unworn and unerupted as well as slightly worn specimens, closely resembles that seen in the Kanjera baboon. They are, however, consistently larger (Table 4, Fig. 10) and show a distinct tendency to the development of extra vertical grooves. The male P_3 differs from that of the Kanjera form by the relative shortness of its 'sectorial' face. The male and female canines are essentially the same as those of the Kanjera baboon, but the male teeth, to judge from the unerupted crowns, were even lower-crowned, relative to the general size of the dentition, than in that form. The incisors are represented by an extensive collection in which permanent and deciduous teeth of both sexes must be present. All are small and slender teeth. There are no specimens resembling the broad median upper incisors of *Papio*, *Mandrillus*, and *Macaca*. The small inter-canine breadth in KNM–OG 0004 confirms that the incisors were small. Many deciduous teeth were present in the collection, but were not examined in detail for the present study.

Forelimb

The *scapula* is represented by four fragments, all rather small. (KNM–OG 1454, 1456, 1457, 1458). All are from the distal end, and include the glenoid fossa and part of the neck. In two specimens a small part of the root of the scapular spine is preserved, and this appears to be closer to the surface of the glenoid cavity than in either the modern or Kanjera series. The glenoid cavity itself may be rather shallower than in the Kanjera and modern specimens, but this appearance may be due to erosion of the articular surface in the Olorgesailie fragments.

The *humerus* is represented by seven specimens.

1. 2993. An immature left humerus, complete apart from the proximal epiphysis and some erosion of the distal extremity.

2–3. Two proximal epiphyses.

4, 5 & 6. KNM–OG 1455, 1459, 1460 (FU 1–3/UL). Three fragmentary distal extremities.

7. KNM–OG 1461. The distal end of a right humerus, with part of the shaft.

In both proximal epiphyses the articular surface appears to be rather flatter than in the modern series or the Kanjera specimen. The distal extremities show the usual cercopithecoid features such as a deep anconeal fossa (probably perforate in life in FU 2/UL). Where the ulnar epicondyle is preserved it is clearly turned backwards as in the modern terrestrial monkeys, but none of the specimens is sufficiently well-preserved for the index of articular breadth to be calculated. None of the specimens with part of the shaft preserved has a prominent brachioradialis flange, and the almost complete specimen shows the straight shaft typical of baboons.

No. 1 is probably from a subadult male individual; 4, 5 and 6 are either from females or from younger juveniles.

The overall length of a male humerus can be estimated by comparing the position of the insertion of the tendon of M. teres major in No. 1 and in male geladas, at a value between 285 and 295 mm. The most complete of the smaller specimens, possibly representing an adult female (No. 5) has a distal articular surface 36 mm in

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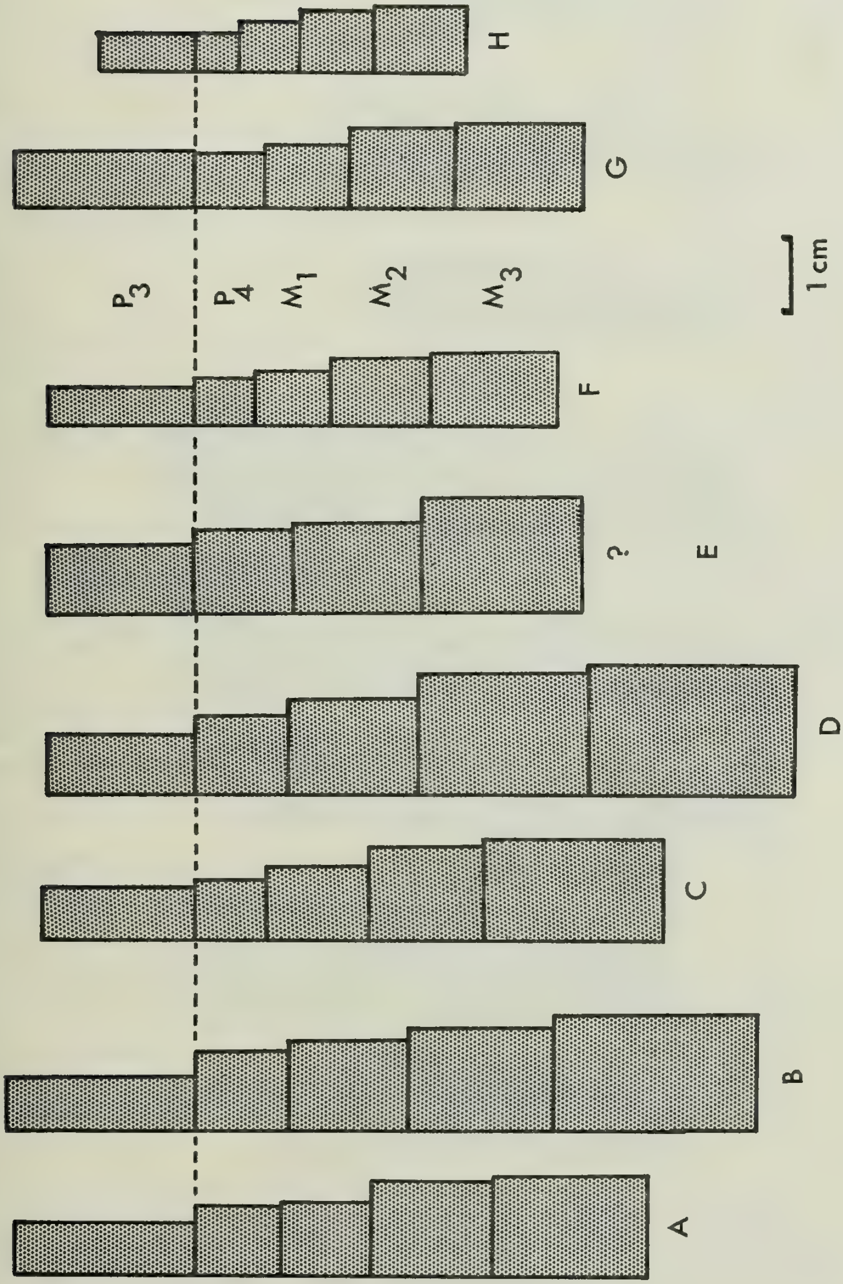
FIG. 10. Size and proportions of lower cheekteeth in *Theropithecus* and *Papio* males. Sides of rectangles represent length and (anterior) breadth of tooth. a. *T. darti darti* (Makapan). b. *T. darti danieli* (Swartkrans). c. *T. oswaldi oswaldi* (Kanjera). d. *T. oswaldi mariae* (Olorgesailie). e. *T. oswaldi leakeyi* (Olduvai IV) (M_3 unknown). f. *T. gelada*. g. *Papio ursinus* (N = 30, Freedman, 1957) (Largest extant *Papio*). h. *P. cynocephalus kindae* (N = 7) (Smallest extant *Papio*).


P3
P4
M1
M2
M3
1 cm
A
B
C
D
?
E
F
G
H

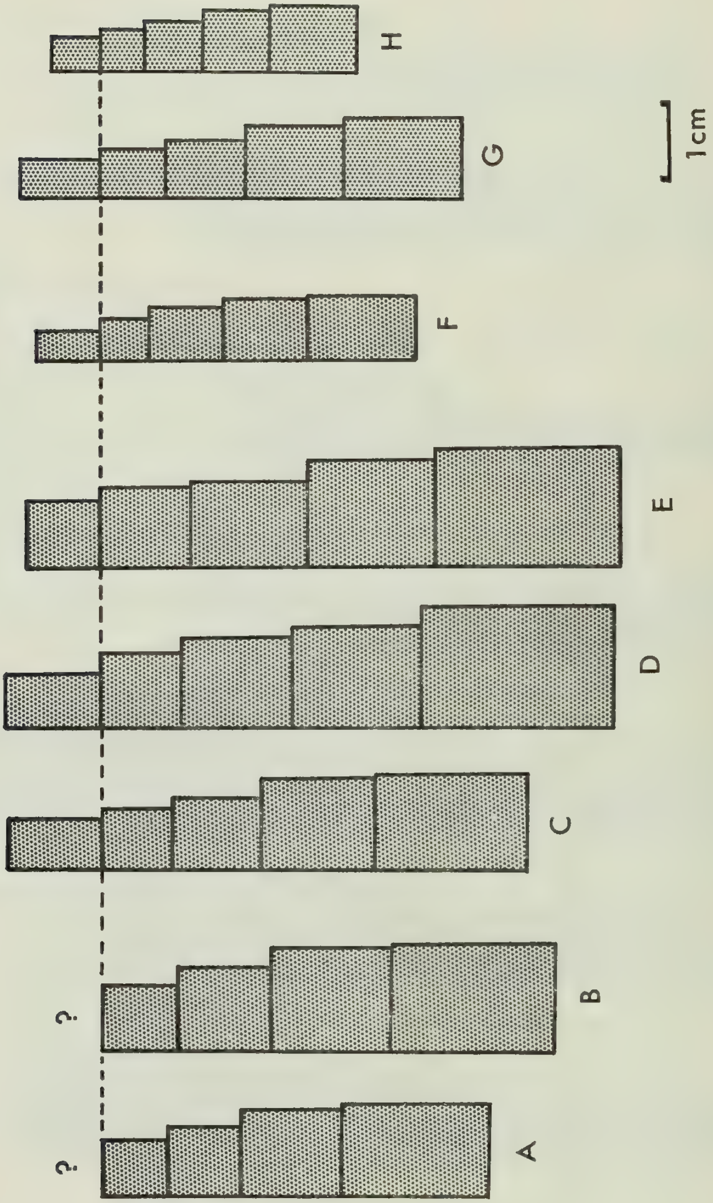


FIG. 11. Size and proportions of lower cheekteeth in *Theropithecus* and *Papio* females. Sides of rectangles represent mean length and (anterior) breadth of tooth. a. *T. darti darti* (Makapan). b. *T. darti danieli* (Swartkrans). c. *T. oswaldi oswaldi* (Kanjera). d. *T. oswaldi mariae* (Olorgesailie). e. *T. oswaldi leakeyi* (Olduvai IV). f. *T. gelada*. g. *Papio ursinus* (N = 7, Freedman, 1957). h. *P. cynocephalus kindae* (N = 17).

breadth; if its overall length was in proportion, this would have been 235 to 245 mm, judging from the relationship between these two dimensions in the male specimen.

Seven fragments of *radii* are preserved: two isolated proximal epiphyses; three more proximal ends, two lacking the epiphyses (OG–1463, 1465, 1466); part of a large but immature radial shaft (OG–1464) and the distal end of a left radius, including the fused epiphysis and part of the shaft (OG–1462).

None of the specimens shows any features to distinguish it morphologically from those of other cercopithecoids such as *Mandrillus*, *Theropithecus gelada*, *Papio* and the Kanjera *Simopithecus*. In the immature specimens the volar surface is less deeply excavated. The lateral curvature of the last specimen listed was probably rather less than that of the Kanjera specimen (M 11544) resembling *Theropithecus gelada*.

No estimate of the unbroken length of the mature bone can be obtained from these fragments.

The *ulna* is represented by four specimens, KNM–OG 1467, 1468. Between them they include the complete proximal extremity and about three-fifths of the shaft. All of them show features resembling *Papio*, *Theropithecus gelada* and the Kanjera *Simopithecus*.

The radial articular facet (three specimens) is deep-set, and the articular surfaces of the anconeal and coronoid processes face largely in a medial direction. The olecranon process is sufficiently well preserved in two specimens for its inclination to the shaft to be apparent, although it is not possible to measure the angle of inclination exactly because the region of the sigmoid notch is damaged and the shaft incomplete. However it is clear that the olecranon was very strongly reflexed, even more extremely than in most individuals of living baboon genera.

Both the *carpus* and the *metacarpus* are well-represented in the Olorgesailie series. It is hoped to make their description the subject of a future publication.

Hindlimb

Eleven separate specimens are present in the collection which can be attributed to the *femur*.

1. KNM–OG 1088 (MS 3991). An adult, right femur, complete apart from some erosion of the surface.
2. KNM–OG 1090 (1731). The proximal end of a right femur, with part of the shaft, the posterior surface of the head, and the greater trochanter slightly eroded.
3. The proximal end and part of the shaft of a right femur, rather distorted and damaged in the region of the greater trochanter.
4. KNM–OG 1470. Part of the proximal end of a left femoral shaft, including the lesser trochanter.
5. KNM–OG 1471. Part of the proximal end of a left femoral shaft, with the surface somewhat eroded.
6. The proximal end and part of the shaft of a left femur, somewhat eroded.
7. The head and neck of a right femur, poorly preserved.

8, 9. Unfused ephiphyses of the femoral head.

10. KNM–OG 1469. The distal end of a femoral shaft, probably left.

11. A fragment of the distal extremity, with one condyle and part of the patellar surface.

The femur of the Olorgesailie *Simopithecus* closely resembles that of the Kanjera form, apart from its greater size. The neck is rather short and broad, the shaft short, stout, strongly marked by muscular attachments, especially those of the adductor group, and showing rather strong anterior convexity. The dimensions of the specimens are shown in Table 9.

Of the specimens upon which meaningful measurements can be taken (1, 2, 3, 4, 6), No. 1 is probably female; the rest are larger and probably male. The overall length of No. 1 is 232 mm. The breadth of No. 2, along the axis of the neck, is 127·9% of the same dimension in No. 1. (No. 3 is closely similar to it). If the length dimension was proportional to this, it was about 297 mm.

The *tibia* is represented by six specimens (KNM–OG 1472, 1473). The most complete of these is an immature right tibia entire apart from the epiphyses. A further specimen, of the left side, has a complete distal extremity. The remaining four are parts of the shaft. At least one is from an immature individual, showing the distal ephiphyseal surface.

The tibia is relatively short-shafted with massive extremities. As in other Cercopithecoidea the shaft has slight convexity towards the lateral side, and is transversely flattened, but does not have a sharp anterior border.

Being immature, the specimens do not show prominent muscular marking. In two specimens, however, an elongated muscle-scar can be seen, immediately medial to the line of the interosseous membrane, which probably represents the area of the origin of M. tibialis posterior.

The dimensions of the tibial fragments are shown in Table 10. None is sufficiently complete to permit reconstruction of the adult, unbroken length.

The *tarsus* is represented in the Olorgesailie collection by several specimens of each bone. Of these, the first and second cuneiformes and the cuboid are of particular interest from the point of view of the locomotory adaptations of *Simopithecus*.

One of the five specimens of *Cuneiform I* (KNM–OG 1474, 1475, 1476, 1477, 1478) is rather larger than the rest, but all have a similar shape and disposition of the articular facets. From the medial aspect, the most striking feature is the relatively small size of the projection of the distal articular surface superior to the body of the bone (the 'beak') indicating that the hallux was relatively small. In this feature *Simopithecus* is even more extreme than any of the modern terrestrial genera.

In a number of specimens the articular surface for the base of the hallucal metatarsal can be clearly seen; it resembles that of *Theropithecus gelada* closely in shape, appearing vertical rather than medially convex from the distal aspect, and with very little expansion on to the medial face of the bone.

From the medial aspect, the inferior margin of all five specimens is evenly convex, unlike any individual of the comparative series of modern genera.

The lateral aspect of the first cuneiform bears the same arrangement of articular facets for the second cuneiform and the base of the second metatarsal as in living cercopithecoids. The two facets on the 'beak' are relatively much smaller than those of the modern arboreal and semi-arboreal genera, and also than *Papio*, agreeing in relative size with those of *Theropithecus gelada*.

Cuneiform II is represented by three specimens. One of these, from the left side (KNM-OG 1479), is intact apart from some damage in the region of the tuberosity, and the details of the articular surfaces can be clearly distinguished.

The distal surface is deep relative to its breadth, and is approximately symmetrical about its long axis, the condition also seen in *Theropithecus gelada*, among modern genera. In those forms which have a larger hallucal metatarsal, and hence a more extensive 'beak' on the first cuneiform, the medial margin of the proximal face of the second cuneiform is much longer than the lateral, in order to support the large 'beak'. The morphology of the lateral surface shows no remarkable features, but that of the medial surface reflects the reduction of the 'beak' of the first cuneiform in the relatively very small size of the anterior articular facet; this is much less in anterior-posterior diameter than the interval separating it from the posterior facet (Fig. 12).

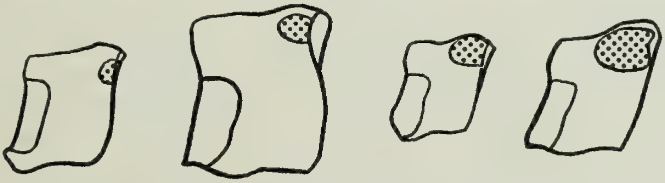


FIG. 12. Medial aspect of right cuneiform II. Left to right: *T. gelada, T. oswaldi mariae*, (Olorgesailie), *Cercocebus atys, Mandrillus leucophaeus*. Note variation in relative size of facet for 'beak' of cuneiform I (Stippled)

Two specimens of the *cuboid* are present in the collection, both somewhat damaged, but between them representing the whole bone (KNM-OG 1480, 1481). Both are clearly of the highly asymmetrical shape seen in *Theropithecus gelada*, with the medial face very much less extensive than the lateral. A distinct facet for the sesamoid of M. peroneus longus is present, but this is small relative to the size of the bone.

The *metatarsus* is represented by a number of specimens, of which the following are complete enough to be of descriptive value.

The *first metatarsal* is represented by a single, complete and evidently mature specimen in which the epiphyses are fused (KNM-OG 1482). It is of the left side. The head resembles that of *Theropithecus gelada* rather closely; there are no large, projecting flanges on either side of the articular surface such as are found in *Papio*, *Mandrillus* and the arboreal genera, and which in these forms support the large sesamoids of the long hallucal flexor. The fossil also resembles the gelada in having the head inclined slightly but distinctly medially. The functional significance of this feature is obscure. The base has no large scar marking the area of insertion of the tendon of the M. peroneus longus, again in agreement with *Theropithecus gelada* and contrasting with the condition seen in other, less terrestrial forms, and the proximal articular surface is more vertically elongated, less curved, than in *Papio* and *Mandrillus*, matching the shape of the distal articular surface of the first cuneiform.

In size, the specimen is comparable to that of a modern *Mandrillus*. Its size relative to the rest of the foot cannot be expressed exactly, since it was not associated with any of the remaining metatarsal specimens, most of which represent immature individuals. These specimens are all very much larger than the corresponding bones in the mandrill, however, suggesting that the first metatarsal was in fact relatively small in the fossil form. This fact may be quantified by expressing the length of the first metatarsal as a percentage of the breadth of the proximal surface of the cuboid, of which two specimens are known from Olorgesailie. Both of these have a breadth of approximately 21 mm giving an index of 229, a very low figure when compared with values obtained for modern genera: *Theropithecus gelada*, 253; *Papio*, 284; *Mandrillus*, 300; *Cercocebus*, 305. It might be argued that an artificially low value obtained for the Olorgesailie form was due to a sex difference between the specimens, the two cuboids representing males, while the first metatarsal was from a female individual. In this case the error could be compensated by multiplying the metatarsal length by 5/4, a reasonable expression of the amount of sexual dimorphism seen in the long-bones of *Simopithecus*. The index derived from the corrected figures is 286, which is close to the value obtained for *Papio*, and still well below that of more arboreal forms. In fact, it is unlikely that the first metatarsal was derived from an individual much smaller than those from which the cuboids came; the size of its proximal articular facet corresponds in size to the distal articular facets of the *largest* first cuneiformes, which are themselves compatible in size with the cuboids.

The *second metatarsal* is represented by two specimens, one of each side, both consisting of the proximal end and the shaft, broken short close to the distal extremity, probably at the epiphyseal line (KNM–OG 1483, 1484). Both are therefore probably from immature animals.

The shaft is very short and stout, and exhibits rather marked lateral convexity. The proximal articular surface is extremely deep and transversely narrow, being most closely approached in this feature by *Theropithecus gelada* among the comparative series. The same surface also resembles that of the terrestrial monkeys in being almost symmetrical about the longitudinal plane of the bone, but the condition is less extreme than in the gelada or in the Olduvai specimens described below, most closely approaching *Papio*. The facets on the lateral side of the base resemble the general condition in living monkeys, but those of the medial side resemble *Theropithecus gelada*, and differ from *Mandrillus* and the arboreal genera, in that the superior facet is subequal to, and not larger than, the inferior.

The *third metatarsal* (KNM–OG 1485, 1486, 1487, 1488) is represented by four specimens, three left and one right; all consist of proximal extremities from which the inferior part is missing, together with a variable amount of the shaft. One specimen, of the left side, extends as far distally as the line of the distal epiphysis. All are probably immature.

Although the full depth of the proximal articular facet is not present, it was obviously extremely narrow and deep. The arrangement of the facets of articulation on the lateral and medial surfaces of the base is as in other cercopithecoids. From the dorsal aspect, the dorsal surface of the base extends proximally in a wedge-shaped process; this is long and acutely pointed, as in *Theropithecus gelada*. The shaft is again very stout, and is marked by strong ligamentous tubercles at the proximal end. The dorsum is flat, and the angulation between it and the sides of the shaft is sharp.

The *fourth metatarsal* is represented by eight fragments, four of each side (KNM–OG 7493, 1494, 1495, 1496, 1497, 1498, 1499, 1500). Most are rather badly damaged, but one has the shaft complete as far as the distal epiphysis.

The shaft is stout, and marked with extraordinarily strong ligamentous impressions. None is sufficiently intact to permit the depth and breadth of the proximal articular surface to be measured accurately, but this was obviously again very narrow and deep. The arrangement of articular facets on the proximal extremity is as in other cercopithecoids.

Four specimens of the *fifth metatarsal* are included in the collection, two from each side (KNM–OG 1489, 1490, 1491, 1492). All consist of proximal extremities, one (of the right side) with the whole of the shaft and part of the head.

The shaft shows moderate medial compression and some medial convexity, but both conditions are less developed than in *Theropithecus gelada*. The shaft is short and stout, also unlike *Theropithecus gelada* in which it is slender, specially relative to those of the other metatarsals.

The facet for the fourth metatarsal is as in other monkeys. The tubercle on the lateral side of the base (for the insertion of M. peroneus brevis) is very massive and

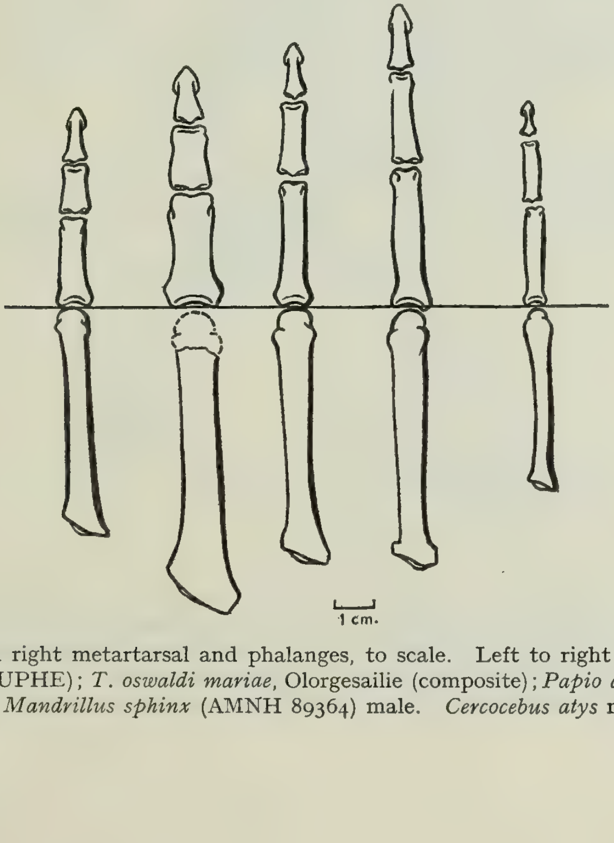


FIG. 13. Third right metartarsal and phalanges, to scale. Left to right: *Theropithecus gelada* male (UPHE); *T. oswaldi mariae*, Olorgesailie (composite); *Papio anubis* (AMNH 82906) male; *Mandrillus sphinx* (AMNH 89364) male. *Cercocebus atys* male.

prominent in all the specimens, resembling the condition seen in *Theropithecus gelada*.

The best preserved of the specimens of metatarsals II–IV, all of the left side and at a similar stage of maturation, probably represent a single foot (KNM–OG 1484, 1485, 1493, 1491). When articulated, they form a very short, broad metatarsus, with a deep proximal articular surface (Fig. 14). Both of the first two features contrast strongly with the elongated, narrow metatarsus of *Theropithecus gelada* and some species of *Papio* (e.g. *P. cynocephalus*), and resemble most closely the more thickset species of the latter genus, such as *P. anubis*, although even these are far less extreme in robusticity than the fossil.

Phalanges are well represented in the Olorgesailie collection (KNM–OG 1501–1520). Unfortunately, as no specimens were associated, and material of many individuals of both sexes is known to be present, there is no means of distinguishing manual from pedal phalanges, or of identifying phalanges of a particular digit (apart from hallux or pollex).

Eleven proximal phalanges are known, of which one is clearly of a first digit, probably the hallux. All are extremely short and stout, exceeding even the gelada in this feature. Specimens sufficiently well-preserved for their relative robusticity to be shown graphically by plotting their length against their basal breadth are shown in Fig. 15. All are quite different from the modern arboreal genera, and exceed even *Theropithecus gelada* in the value of the index.

The middle phalanges, of which nine are known, agree in shape with the proximal, indicating even shorter and stouter digits than are seen in *Papio* and *Theropithecus gelada*. The distal phalanges, represented by four specimens, of which one is probably of the pollex, are of the shape normal in Cercopithecoidea.

C. OLDUVAI, UPPER BED II SERIES

Accounts of the geology and stratigraphy of Olduvai gorge, northern Tanzania, were published by Reck (1926) and Leakey (1951) while the preliminary results of

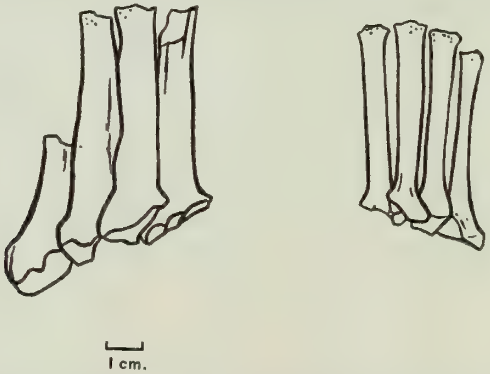


FIG. 14. Articulated juvenile metatarsus, excluding metatarsal I. Left: *Simopithecus* (Olorgesailie). Left foot, diaphyses of all but metatarsal V virtually complete. Right: *Papio* sp., male (UPHE). Right foot. Epiphyses removed. Note close appression of metatarsals of fossil specimen.

more detailed geological surveys have been published by Pickering (1958, 1960, summarized by Bishop, 1963) and Hay (1963, 1967). The latter author summarizes the results of his own and previous studies as follows:

> 'Bed I at Olduvai is a conformable sequence of lava flows and varied sedimentary deposits that extend upward from a welded tuff overlying the Precambrian basement to the top of a widespread marker bed. Bed II is a sequence of lacustrine clays and laterally equivalent fluvial, eolian and pyroclastic deposits. Bed III comprises alluvial deposits and a laterally equivalent assemblage of fluvial, lacustrine and eolian beds. Bed IV can be widely subdivided

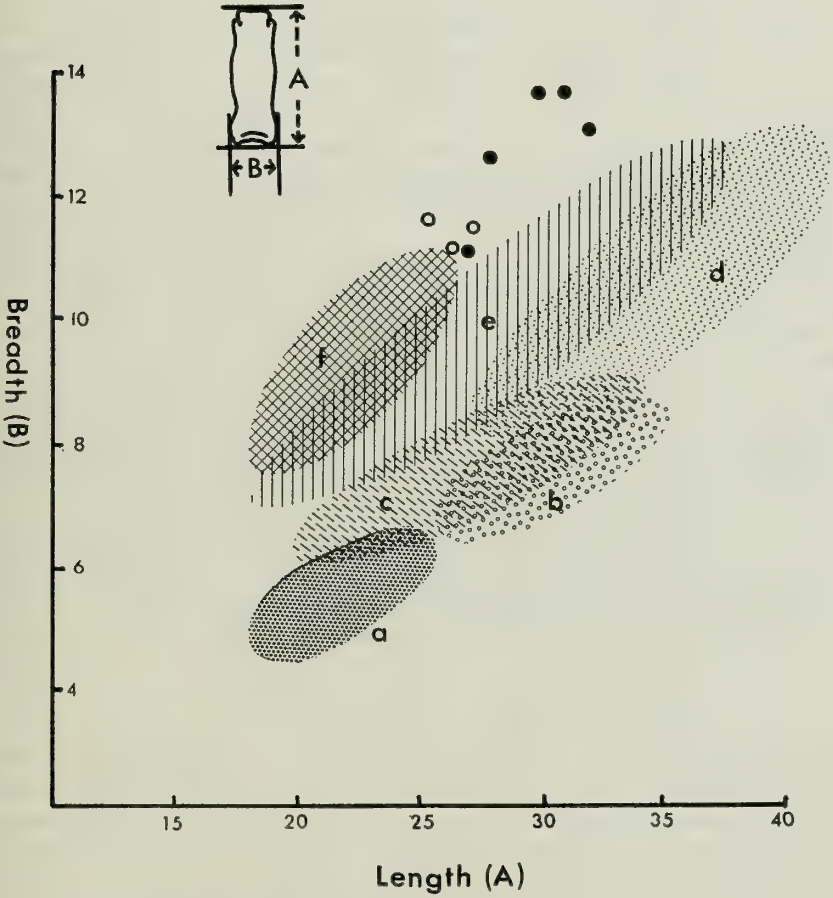


FIG. 15. Basal phalanges of hand and foot; breadth plotted against length, with selected percentiles of index Breadth/Length. Shaded areas represent observed range of phalanx shape in each extant genus. a. *Cercopithecus* (N = 40). b. *Cercocebus* (N = 40). c. *Macaca* (N = 40). d. *Mandrillus* (N = 40). e. *Papio* (N = 80). f. *T. gelada* (N = 40). Open circles: *Simopithecus*, Olduvai. Solid Circles: *Simopithecus*, Olorgesailie.

> into a lower unit of fluvial clays, sandstones and conglomerates and an upper unit of eolian tuffs. Although moister than that of the present day, the climate was relatively dry throughout much of the time that these beds were deposited. Semi-desert or desert conditions rather like those of the present day may have prevailed at least twice. Tectonic movement seems to have taken place between the deposition of Beds III and IV'.

Leakey (1963) emphasises that a stratigraphical, faunal, cultural and probably climatic break exists between the upper and lower parts of Bed II. A series of Potassium/Argon dates for Olduvai material (Leakey, Evernden and Curtis, 1961, Hay, 1963) appear to confirm the existence of this hiatus, and also indicate the very long time span of the Olduvai deposits – greater than $1{\cdot}7 \times 10^6$yrs. Later fieldwork by Hay (1967) indicates that the Bed I–Lower Bed II series is separated from the upper sequence by major tectonic events associated with Rift Valley faulting, which destroyed the permanent saline lake. This was replaced by a 'broad, playa lake and alluvial plain' (Hay, 1967).

As Leakey (1963, 1965) has pointed out, the value of many of the earlier collected specimens is reduced by their being assigned to an incorrect horizon, or none at all. This applies to many of the British Museum specimens which are marked merely 'Olduvai'.

A further complication factor is the presence at Olduvai of at least two other Cercopithecoidea as well as *Simopithecus*; there is a distinct possibility that skull fragments or postcranial bones not directly associated with teeth have been wrongly attributed.

By far the greatest amount of Olduvai *Theropithecus* material is derived from BK II, a site in the latest layers of Bed II fossiliferous deposit that consists of the clay infilling of a former stream-channel (M. D. Leakey, 1967). It includes cranial, dental and postcranial material, mainly in a fine state of preservation, though somewhat fragmentary. A second, smaller, series consisting of well preserved postcranial bones, is derived from site SHK II, which is believed to be of a broadly similar, but slightly earlier, age (M. D. Leakey, 1967). Although its attribution to *Theropithecus* must be provisional until confirmed by associated cranial or dental material, it is close in structure and size to the BK II series.

Skull

a. M 18772, BK II 9.V.35. (Plate 14a)

A frontal, complete apart from the extreme lateral part of each side. The posterior surface of the fragment, at least in the region of the bregma, corresponds exactly with the line of the coronal suture. The temporal lines are sharp and prominent, and are situated far up on the superior surface of the frontal. The supraorbital torus is rather heavy and rounded, and divided in the centre by a shallow depression.

b. BK II 1957 (Plate 17a)

A skull, probably female, almost complete apart from the facial region and the mandible. No apparent post-mortem distortion.

Death was probably due to injuries associated with a depressed fracture of the right parietal and frontal region. The depressed area is bounded anteriorly by a semi-circular fracture of the bone, but posteriorly by a flexure of the bone which must have occurred when this was in a fresh condition. A pair of parallel, shallow grooves runs antero-posteriorly across the depressed section of bone. If, as seems likely, the injury was caused ante or ad mortem by a blow from a missile or hand-held weapon, this blow probably fell from the right side.

In general shape, the braincase resembles that of the Kanjera *Simopithecus*: its profile between the glabella and inion is rather flatter than that seen in *Theropithecus gelada* and resembles the condition in *Papio.* The temporal lines, which appear to be single, are raised and come close to meeting about the bregma, but then run parallel to about one centimetre from the inion, where they begin to diverge, finally intersecting the nuchal line about a centimetre each side of the inion. In the region where the two lines are close together there is marked keeling of the cranial vault. The supra-orbital tori resemble those of the Kanjera specimens in shape, rather thick and shelf-like, and divided by a shallow rounded depression. The supra-orbital notches are deep. The orbits themselves are incomplete, the specimen being broken across the nasals and at the zygomatico-frontal suture. The roof of the right orbit, and part of the left, are preserved, and it can be seen that the optic foramen resembles that of modern cercopithecines.

The inion is prominent, and higher than the adjacent occipital crests, which widen laterally to become confluent with the temporal end of the zygomatic arches. There is scarcely any lateral projection of the mastoid processes beyond the line of the occipital crests, as in the Kanjera *Simopithecus* and *Papio*, but unlike the gelada in which the mastoids are strongly laterally-projecting. The nuchal region of the occipital bone is closely similar to that of *Theropithecus gelada* in shape; that of *Papio* (and still more that of *Mandrillus*) is more acutely angled posteriorly when viewed from the basal aspect. This may be related to the posterior disposition of the main mass of the fibres of the temporal muscle in these forms. The foramen magnum and the occipital condyles present no unusual features.

The whole of the base of the skull anterior to the foramen magnum is broad relative to its length. This shape is reflected in the width of the basilar part of the occipital. The pair of fossae situated on its external surface to either side of the midline, which may be associated with the areas of insertion of the Mm. longus and rectus capitis, are more extensive than in living genera, occupying most of the basal surface. This feature may be related to the shortness of the skull-base, but also perhaps to an unusually large development of the muscles concerned. The basal suture was open at the time of death.

The petrous and tympanic parts of the temporal are somewhat damaged, but their general appearance is as in *Papio* and *Theropithecus gelada.* The external auditory meatus faces more directly laterally, and less posteriorly and superiorly, than in modern *Papio*, but the feature is less marked than in the Kanjera male.

The articular region is shaped much as in the living genera, and is without the distinct laterally-facing surface seen in the Kanjera male. The post-glenoid tubercle is long and massive, and as in the Kanjera male, it is in close contact with the external auditory meatus, reflecting again the shortness of the skull-base, a feature directly opposed to the condition in forms of *Papio* and *Mandrillus* of comparable size.

Only the posterior parts of the pterygoid fossae are preserved, and of these only the right has been developed from the matrix. The characteristic line running up the medial surface of the lateral pterygoid plate, as in the Kanjera specimen, can be distinguished.

c. BK II (Plate 15a and b)

An almost complete juvenile female corpus mandibulae (figured in Leakey and Whitworth, 1958, as *S. oswaldi*). On the left side the incisors, canine, premolars and first two molars are fully erupted and in occlusion. The third molar had not started to break through the alveolar bone at the time of death, but owing to post-mortem damage is visible in its crypt. On the right side, the incisors, canine, premolars and first two molars are present and in occlusion. The jaw is broken short immediately posterior to the second molar, but the anterior and inferior surfaces of the crypt of M_3 are present. The specimen is somewhat cracked and probably slightly expanded by matrix-filled cracks. A slight asymmetry of the two halves suggests that some post-mortem distortion has occurred.

The incisors show moderate wear with their tips worn to a flat surface; the canines show only very slight wear. The third premolars are unworn apart from an extremely small wear-facet on the tip of the higher cusp of each. The fourth premolars have small wear-facets on both cusps. M_1 is moderately heavily worn, with a single area of dentine exposed over its whole surface. The second molars are unworn, apart from a small wear facet on the anterior buccal, and an extremely small facet on the posterior buccal cusp. The age of the individual at death was therefore probably rather greater than that of the Kanjera juvenile female (F 3398).

The jaw is rather broader and more massive than that of the Kanjera individual, and the superior symphyseal shelf is relatively longer, extending backwards, when the jaw is held with the occlusal plane horizontal, to the level of the posterior half of P_4. The inferior symphyseal ('simian') shelf has much the same extent as in F 3398, reaching to the anterior cusps of M_1. No mandibular fossa is present. The inferior surface of the symphyseal region is flat and triangular. Two mental foramina are visible on the left side, beneath the anterior part of P_4.

d. Old. BK II Ex. 1953/117

A fragment of the posterior end of the left side of a mandibular corpus, with M_2 and the roots, broken short, of M_3. M_2 shows moderate wear; M_3 was perhaps not fully erupted at the time of death.

e. M 14953 BK II Red bed (Plate 15c and d)

Mentioned by Hopwood, (1936). Illustrated (as male) by Leakey and Whitworth. The left side of a corpus mandibulae, with the three molars and P_4 present and reasonably well-preserved. P_3 is represented only by the posterior part of the tooth and its root. The impression of the anterior root of P_3 is however visible on the surface of the broken alveolus; from the size of this it seems likely that the individual was female, rather than male as stated by Leakey and Whitworth. The corpus itself is badly cracked and distorted, but the position of the superior symphseal shelf is determinable; this extends posteriorly as far as the posterior part of P_4. The third molar is newly erupted, showing wear on its anterior lingual cusp only. M_2 and P_4 are moderately worn, while M_1 is heavily worn.

f. M. 18779 (Plate 14d and e)

(This specimen is tentatively included with the Upper Bed II series. The label enclosed with it stated that it comes from Broken Hill; however, no non-human primate cranial material is known from this site (Leakey 1956). It bears the inscription 'Old-y II' and is hard and black, quite different from the friable, pinkish-red Broken Hill postcranial bones (M 18776, M 18777, M 18778).)

A fragment of a right maxilla, female, with the canine and two premolars *in situ*. The anterior margin of the fragment is probably the maxillary-premaxillary suture. A moderately large wear-facet is present on the posterior face of the canine; the premolars are scarcely worr, with the dentine exposed only at the tips of the cusps. The buccal root of P^4 was probably exposed on the maxillary surface before death.

As in specimens from Kanjera there is a complete absence of maxillary fossae.

g. M 14681 (Plate 14b and c)

Described by Hopwood (1934) as *S. leakeyi*. This specimen is also tentatively referred to the Upper Bed II form. Part of a left maxilla with M^2 and M^3 in position, the alveoli of M^1–P^4 and part of the posterior wall of the canine socket preserved. The small size of the canine indicates a female individual. M^2 shows moderate, and M^3 slight to moderate wear. The buccal roots of the second molar were probably slightly exposed. The posterior palatine foramen is at the level of the posterior cusps of the third molar, and situated close to the base of the alveolar eminence. With the occlusal surface horizontal, the root of the zygoma is above the anterior cusps of M^3.

Teeth

The teeth of the Bed II *Theropithecus* agree with those of Kanjera and Olorgesailie in general structure. The distinctive pattern of grooves clefts, and fossae is well developed in the cheek-teeth, while the upper and lower canines of the females are relatively small. The small size of the incisors is well documented by the juvenile female mandible, 'c' in the descriptive list. No male anterior teeth were available for study.

In size, those few teeth which can be readily sexed are comparable to the low end of the Olorgesailie range.

Postcranial Material

As mentioned, at least two cercopithecoids apart from *Theropithecus* occur at Olduvai. All specimens which could not be excluded from the genus on grounds of size or morphology are described here; some may well be wrongly attributed.

The *humerus* is represented by three specimens.

1. 1384 5K IIE. The complete distal extremity and about three-fifths of the shaft of a left humerus. There is some damage to the anterior surface of the shaft, and very slight erosion of the sharper edges of the distal extremity.

The shape of the specimen is much as described for the Kanjera baboon, but strong spiral grooves, which in living forms are occupied by the M. brachialis, are present. In addition, the brachioradialis crest is rather more prominent than in the Kanjera specimens, though less so than in *Mandrillus* among the modern series.

2. BK II 118

The distal extremity and about three-fifths of the shaft of a left humerus, well-preserved apart from general loss of detail through erosion of the surface, especially of the distal end. Both epicondyles are broken.

The shaft appears exceptionally straight, from both lateral and anterior aspects. The anconeal fossa is perforated, and was probably in this condition in the live animal. The brachialis-brachioradialis crest and flange are low as normally in *Theropithecus*, and no spiral grooves are present.

3. SWK II F 2953

A well-preserved fragment of the distal end of a right humerus. It resembles 1384 BK IIE in morphology, but the spiral grooves are lacking, and the ulnar epicondyle is rather larger and more medially projecting.

The dimensions of all three specimens are included in Table 6. Both specimens (1 and 3) for which the index of relative epicondylar breadth could be calculated had a lower value than was found in the Kanjera *Simopithecus*, and also fell outside the range of modern *Papio* and *Theropithecus gelada*, lying within the range for *Mandrillus* (Fig. 5).

Two specimens may be attributed to the *radius* of *Simopithecus*.

1. Is 1941

A fragment of the proximal end of a left radius. The bicipital tuberosity is prominent and the volar surface rather deeply excavated.

2. BK II 1953/54

The head, neck, and part of the proximal end of the shaft of a left radius. Surface detail is well-preserved. The bicipital tuberosity is distinct. The surface of insertion of the M. supinator is marked off from the volar surface by a strong raised fascial line. Its surface is marked with faint parallel grooves probably representing the positions of the fibres of the supinator. The interosseous margin is prominent, and the volar surface rather deeply excavated.

The *femur* is represented by two proximal and two distal extremities.

1. BK II Surface 693 1953

The complete proximal end of a right femur with only slight damage to the head. The shaft is broken obliquely below the level of the lesser trochanter, so that more of the medial than the lateral surface is preserved. The morphology of the fragment resembles that of Kanjera specimens, having a rather short, broad neck, and massive greater trochanter, the tip of which faces more directly medially than in most living Cercopithecoidea, and almost overhangs the margin of the head. A deep pit, distal to the lesser trochanter on the posterior surface and extending to the broken margin of the fragment, probably represents the origin of the most proximal part of the adductor mass.

2. SHK II E 1203

The proximal end of a right femur, together with part of the posterior surface of the shaft, the anterior surface mainly absent. This specimen resembles the last, except that the muscular markings on the lateral surface of the greater trochanter are stronger, perhaps indicating a rather older individual.

3. BK II E 1383

The distal end of a right femur, with part of the shaft.

4. Olduvai (R)

Distal end and part of the shaft of a left femur.

These two specimens are closely similar in shape and size, and may perhaps be attributed to the same individual. The shape of the shaft and the muscular and tendinous impressions on the distal extremity resemble those of modern Cercopithecoidea. The most remarkable feature of both is the extraordinary orientation of the condyles on the shaft, which leads to a degree of 'kneeing-in' equivalent to that regularly seen in hominid femora. The feature is highly variable among cercopithecoid monkeys, more so, apparently, than among either the Pongidae or the Hominidae; occasional individuals (e.g. a specimen of *Mandrillus* in the collection of the Primatology Unit, Royal Free Hospital) have as much convergence at the knees as is seen in the Olduvai individual.

The dimensions of the femoral specimens are shown in Table 9, p. 41.

No specimens of the leg are known from Olduvai.

The *tarsus* is represented by an associated talus and calcaneus (BK II 63 and 315), and two well-preserved examples of the talus (BK II 1050 and SHK 400). These specimens resemble the corresponding bones of the Kanjera form and are of the shape usual in large, heavily-built quadrupedal monkeys.

Metatarsus and *phalanges* are represented by seven specimens, of which the first four were associated, and are presumably from one individual.

1. BK II 1952 316

The proximal extremity of a second right metatarsal, with part of the shaft, the proximal and lateral surfaces somewhat damaged.

From the proximal aspect, the base appears extremely narrow and deep, more so than any of the modern comparative series, but most closely approached by the gelada. The proximal articular surface resembles that of the modern terrestrial genera, and is quite unlike that of the arboreal and semi-arboreal forms, in being symmetrically T-shaped, indicating little torsion of the second digit in the living animal. The articular facets of the lateral aspect are similar to those of the species in the modern series. The most striking feature of the medial aspect is a prominent tubercle representing the attachment of the interosseous ligament. The articular facet lying postero-dorsal to this, which articulates with a corresponding facet on the 'beak' of the first cuneiform, is relatively small. This agrees with the condition seen in the gelada and Olorgesailie *Simopithecus*, and contrasts with that seen in those (arboreal and semi-arboreal) genera in which a large cuneiform 'beak' supports the massive hallux.

2. BK II 1952 317

The proximal extremity of a right third metatarsal, matching the previous specimen. The styloid process is absent. The bone is marked by strong ligamentous tubercles; the dorsum is flat and the angulations between the dorsal and lateral surfaces sharp, perhaps indicating that the metatarsals were closely appressed in articulation, as in the gelada and the Olorgesailie *Simopithecus*. The wedge-shaped process of the dorsal surface extending proximally is long and acute, again as in the gelada among modern forms, and unlike the condition in arboreal monkeys. The small, convex facet on the medial aspect (for the second metatarsal) and the larger, concave one on the lateral face (for the fourth) are unremarkable.

3. BK II 1952 318

A whole, well-preserved proximal phalanx, attributable to the foot by its association with the previous specimens, and probably of the second digit. All surface detail, including tendinous grooves, the impressions of the attachment of the flexor sheath, and the outlines of joint-surfaces, are very clearly preserved. Dimensions of this specimen have been included in Fig. 15, in which the breadth of the base of proximal phalanges is plotted against their length. With a breadth exceeding 40% of its length, this specimen is approached in stoutness only by *Theropithecus gelada* among modern monkeys, agreeing with the Olorgesailie specimens.

4. BK II 1952 319

A complete, excellently preserved middle phalanx, probably from the second pedal digit. This specimen again exceeds any of the modern series in its shortness and stoutness, which is only approached by the corresponding bone in *T. gelada*. It is quite unlike the long, slender middle phalanges of the more arboreal monkeys.

5. SHK II 286

A third right metatarsal, perfectly preserved apart from a small shaving in the region of the more dorsal of the two facets for metatarsal IV. The specimen is considerably smaller than BK II 1952 317 and so is probably from a female individual.

The most striking feature of the specimen is the relative shortness and stoutness of the shaft, and the relative massiveness of the proximal extremity. In particular, the tendinous markings of the proximal end extend further distally on to the shaft than in modern forms. The proximal articular surface is deep and narrow, and as in BK II 1952 the base extends proximally in a long and acutely wedge-shaped process. The articular surface is flat, rather than convex as in the more arboreal monkeys. The shaft is less strongly angulated than in BK II 1952, resembling the gelada. The morphology of the head region is normal for a cercopithecoid monkey, except that the groove immediately posterior to the articular area on the dorsal surface is exceptionally deep. Such a development of the groove is regular in animals such as those Carnivora which are habitually digitigrade on their hind feet. However, the groove is rather irregular in occurrence among living monkeys, and in them does not appear to be related to posture, so that it would be unwise in the absence of other evidence to infer that the Olduvai *Simopithecus* was habitually digitigrade on its hind feet. The two small facets for the second metatarsal, situated on the medial surface of the base, are separated by a broad, shallow groove, as in other large cercopithecoids. In the smaller monkeys the facets are proportionally larger, and the tendinous groove narrower, a feature probably related to the need for greater tendinous support for the foot in the larger forms. The two facets on the lateral side, for metatarsal IV, resemble those of other monkeys in shape and relative size.

6. BK II 1953/69 and
7. Olduvai (un-numbered)

Two well-preserved proximal phalanges. In the absence of associated material it is not possible to attribute these specimens with certainty to the hand or the foot, but this does not affect the functional implications of their shape; they could only have been derived from a terrestrial form, as can be deduced from their breadth/length ratio, which exceeds 40% in both.

D. Olduvai, Bed I and Lower Bed II Series

Available material antedating the 'faunal break' at Olduvai consisted of two partial mandibles from site DK I, and a damaged talus from HWK. The former is close to the base of the Olduvai sequence, while the latter, formerly believed to lie within Bed I, is now thought to belong to the lower part of Bed II. (M. D. Leakey, 1967).

Skull

a. M 14937 DK I

Part of a right mandibular corpus, with molars and P_4 present. M_1 is very heavily worn, M_2 heavily worn and P_4 and M_3 moderately worn.

b. M 14938 DK I. Mentioned, as *S. leakeyi*, by Hopwood (1936). (Plate 16).

Part of the right corpus mandibulae of an adult female individual, with M_3, P_4, P_3 and the vacant alveoli of the first two molars. The posterior part of the canine root, and the posterior surfaces of the alveoli of the right incisors are also present. The specimen is broken at the symphysis just to the left of the midline, so that the symphysis is shown in cross section. The third molar and the premolars show moderate wear. The superior symphyseal shelf extends posteriorly to the level of the anterior part of P_4, the inferior to the level of the anterior cusps of M_1. The inferior surface of the symphysis is flat. Three mental foramina can be distinguished, about one-third of the distance from the inferior to the alveolar margin, below P_4 and M_1.

The specimen shows several interesting points of difference from the females of the Kanjera, Olduvai II and Olorgesailie forms. There is a distinct, though not deep, mandibular fossa defined superiorly by the flaring alveolar margin below M_1–P_3, and the raised mandibular border in the same region. The mandibular corpus deepens appreciably anteriorly reaching its greatest depth below the mesial cusps of M_1, and the anterior part of the symphyseal shelf is rather more steeply-sloping. In each of these characteristics it is reminiscent of *T. gelada*.

Teeth

All the available teeth of the Bed I baboon are rather badly worn or damaged. The structure of the molars and premolars shows no differences from other populations which could not be attributed to individual variation. (They are somewhat smaller than those of the later, Bed II form).

The bi-incisal breadth in M 14938 can be estimated at about 15 mm, indicating that the incisors showed the reduction in relative and absolute size characteristic of the genus.

Postcranial Material

The single damaged talus from HWK (M 18771) is of the usual form for a large terrestrial cercopithecine.

E. OLDUVAI, BED IV SERIES

Skull

Two mandibular specimens from Bed IV were available.

a. M 14680 Bed IV (Plate 16a and b)

Part of the right side of a juvenile male mandible, described by Hopwood (1934) as the type of *S. leakeyi*. Little is visible of the shape of the mandible, which is very badly cracked. The first molar is fully erupted, and shows light wear. The anterior deciduous premolar is still in position. None of the other permanent cheek-teeth had begun to erupt at the time of death, but the germs of M_2, P_3, P_4 and the canine were fully formed and have been exposed by dissection of the alveolar surface. As in modern genera, the roots of the unerupted P_3 are 'astride' the canine, and both it and P_4 are rotated so that the anterior root is on the buccal side.

b. Old. 1472, 57 Bed? IV, Site JLK; the type of *S. jonathani* Leakey and Whitworth 1958. (Fig. 16)

A mandible, complete apart from some damage to the incisal region. Some post-mortem distortion is shown by the asymmetry of the two halves. The dentition is complete apart from the incisors and the right P_3. All the molars show extreme wear, the first being reduced to little more than stumps. The morphology of the jaw has been described by Leakey and Whitworth (1958). Its most notable features are the massiveness of the corpora, and the relative height of the rami. Leakey and Whitworth draw attention to the more vertical position of the ascending ramus as compared with that of the Kanjera form. In all their illustrations the left side is figured. Owing to post-mortem distortion of the specimen, the ramus of this side

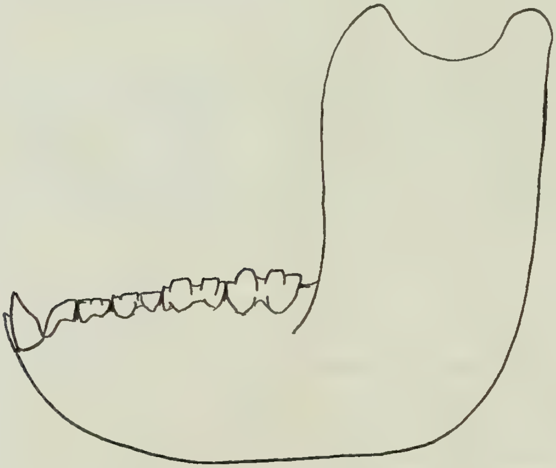


FIG. 16. Reconstruction of jaw from Olduvai IV, type of *Simopithecus jonathani* (Old. 1472, 57).

is rather more vertically disposed than that of the right side, which is angled more like that of the Kanjera baboon. The orientation of the rami in life was probably between that of the left and right sides as presently preserved; this shape is shown in Fig. 16, and does not differ significantly from the orientation of the rami seen in the Kanjera baboon, or for that matter, in *Theropithecus gelada.*

The symphysis shows a similar structure to that of the Kanjera and Olorgesailie specimens, and there is no mandibular fossa.

This specimen is said by Leakey and Whitworth to be female, presumably based upon the relative size of the canine, which is extremely worn, but which can be seen to have been somewhat larger, in cross-sectional area, than P_4. This is unusual for female baboons, in which the lower canine is usually the smaller in area. On the other hand, the tooth is small for a male, and the P_3 (also extremely worn), appears to have been short and scarcely sectorial in form. In view of the tendency towards reduction in the relative size of the male canine and P_3 which is characteristic of the genus, the possibility that the specimen is male cannot be altogether discounted, and is perhaps more likely than the usual attribution.

Teeth

Little remains of the crowns of the cheek-teeth in Old. 1472,57, although enough can be seen of P_4 and M_3 to make its generic identity reasonably certain. Although the incisors are absent, the bi-incisal breadth was clearly very small.

The teeth of M 14680 are well-preserved, and, with the exception of the dp_3, are unworn. The molars resemble those of the Kanjera form, but show all the peculiarities of the genus in exaggerated form. The foveae and clefts are all exceptionally broad and deep. The median buccal cleft is especially deep, and extends behind the protoconid and hypoconid, leaving these cusps standing as partially isolated columns. Similar grooves from the talonid basin and distal fovea cut behind the entoconid. As in one of the Kanjera M_3's the entoconid is divided into a double column, fully on M_2 and partially on M_1. The deep talonid basin is walled lingually by a horizontal enamel ridge which is clearly distinct from the lingual margin. M_1 bears an accessary capsule in the median buccal cleft.

The premolars are rather distinctive in structure, P_4 has a large and deep distal forea, but the mesial forea is extremely reduced. P_3 is of the usual form in male Cercopithecoidea, but is exceptionally short and broad, with a very short sectorial face contrasting with the extensive distal fovea.

The canine crown was not fully exposed, but clearly was small and low, especially as compared to the very large cheek-teeth.

The remaining Olduvai specimens cannot be assigned to a level in the sequence. They comprise:

a. M 19010

The inferior part of mandibular symphysis, broken slightly above the level of the 'simian' shelf. The muscular impressions representing the area of attachment of the platysma are rather strong; the inferior surface shows the usual *Simopithecus* shape.

b. 'Olduvai'

The superior end of a left ascending ramus, complete apart from some damage to the coronid process and the surface of the condyle. The sigmoid notch is shallow, and the condyle apparently shows typical *Simopithecus* features, such as the rather broad, flat, superiorly-facing articular surface, and a depression on the posterior surface of the condyle below the articular surface.

c. The posterior part of a left corpus, with part of the ramus. M_3 is present, its talonid somewhat damaged. Slight wear is present on the tips of all the cusps.

d. Old. 1952 GRCS 694

A fragment of a left horizontal ramus, with the second and third molars in place. M_2 shows moderate wear, M_3 is not fully erupted, and shows wear on the tip of the anterior lingual cusp only.

F. OMO

The series of formations along the lower Omo River, consisting of extensive and richly fossiliferous water-laid deposits, were described by Leakey (1943b) and Arambourg (1947), and have recently been more thoroughly surveyed by Butzer and Thurber (1969). Monkey material was collected and described by Arambourg, (1947) under the name of *Dinopithecus brumpti*. Re-examination of the specimens confirmed the view of Freedman (1957) and Leakey and Whitworth (1958) that they in fact represent a *Simopithecus* (i.e. *Theropithecus*).

Recent collecting in the Omo basin, (Howell 1969 and pers. comm.) has yielded a rich sample of material of Cercopithecoidea, some of which may be referable, or closely related to, *Theropithecus*. It seems not unlikely that these will be found to belong to the species represented by Arambourg's material. The latter comprises:

a. 'Type A'

The posterior part of a left maxilla, with M^2 and M^3. The second molar was fully in occlusion at the time of death, but is only light to moderately worn. The third molar was probably entirely within its crypt at death, but has been exposed by erosion of the alveolar surface. The root of the zygoma is present, and lies approximately above the midpoint of the second molar.

b. 'Type B'

A fragment of the right corpus of a juvenile mandible, containing the root of P_4, the first and second molars complete, and a fragment of the third. The first molar shows moderate wear, the second slight wear only, and the third was unerupted at the time of death, with the tips of the cusps just penetrating the bone of the alveolus. As in *Simopithecus* from other sites, the corpus is very robust at the level of the molars and their roots, but becomes rapidly thinner towards the inferior margin.

c. A fragment of a left corpus mandibulae, with a well-worn M_3.

d. Isolated dental specimens: the unerupted M_2, a worn M_1 and M_3.

The Omo teeth show no peculiarities to distinguish them from the type, Kanjera series, apart from the fact that one, at least, of the two M_3's evidently had a clearly defined tuberculum sextum. In size, they are very close to the female specimens from Olduvai I.

G. KAISO

The Kaiso deposits were described by Wayland (1926), Solomon (1939), and Bishop (1968). The major part of the formation consists of clays, silts and sands with few mammalian fossils. The fossiliferous layers from which the baboon specimen was recovered occur towards the top of the formation in the form of indurated sands, impregnated with ferruginous matter. According to Wayland, the clays were probably desposited during a pluvial period, while the sandy horizons formed during a period of dessication, and represent the site of shallow, drying pools. This view is accepted by Leakey (1951). Solomon and Bishop, however, argue that the clays were probably deposited under swamp rather than lacustrine conditions, and that the sandy horizons were deposited in more open water, with fluctuation reflecting tectonic rather than climatic factors.

The single monkey specimen from Kaiso is a maxillary fragment with right M^2 and M^3, both rather heavily worn. However, the structure of the crown, especially the existence of well-marked lingual and buccal mesial grooves, identifies the genus.

H. MAKAPAN

The geology of the Makapan ('Limeworks') site, situated close to Potgietersrus, Transvaal, has been described by several authors (Dart, 1925, 1952; Bosazza, Adie and Brenner, 1946; Barbour, 1949, King, 1951; etc.): the available evidence was summarized and greatly augmented by Brain (1958), and has recently been reviewed by Butzer (1970). The fossiliferous deposits, which have produced a rich mammalian fauna including *Australopithecus*, consist of the cemented filling of a subsidence-cavern, originally subterranean, in dolomitic limestone. Most of the fossils are derived from the 'Phase I breccia' (Brain 1958), believed to have been formed relatively gradually at a time when the cave entrance was small. It has been suggested (Dart, Brain, op. cit.) that the bones were accumulated at this period by carnivorous animals, (perhaps *Australopithecus*), and Dart (1957) has suggested that many specimens were used by *Australopithecus* in its osteodontokeratic culture. A sudden increase in the size of the cave-entrance was probably the cause of an abrupt change to the deposition of 'Phase II' deposits which include much surface material and few fossils; the latter are indistinguishable from those occurring in the Phase I breccia.

Skull

No original Makapan *Theropithecus* material was available for examination in the present study. It has, however, been fully described and figured by Freedman (1957, 1960), and casts of some of this material were examined.

The material as listed by Freedman consists entirely of cranial and dental fragments; no postcranial specimens are known. No upper jaw fragments are present. A number of teeth isolated or set in small jaw fragments complete the collection.

Fragmentary as it is, the material demonstrated that the Makapan form is clearly separable from the better known East African populations. As Freedman (1957,

1960) observed, the best preserved male mandible (M 626) shows a very distinct mandibular fossa, defined inferiorly by the strongly flaring lower border of the mandibular corpus. This feature is absent in the Kanjera and Olorgesailie forms. Traces of a similar fossa are to be seen in the female mandibular fragment (M 633), though it was evidently less well developed than in the male, as is usual in the females of species in which the fossa occurs. Furthermore, and also unlike the later East African series, the internal surface of the symphysis, instead of being flat, slopes downwards rather abruptly between the premolars again as noted by Freedman (1957, 1960). The shape of the mandibular corpus differs in another respect from that of the Kanjera and Olorgesailie forms. In the female specimen, in which the length of the molar row of 40 mm, the depth of the corpus below the median buccal cleft of M_2 is 38 mm (0.95 of molar length). In the Kanjera female M 11539 comparable dimensions are 42 and 29 mm, giving a ratio of 0·69.

The Olorgesailie and Olduvai I female jaws resemble that of Kanjera with ratios of 0·63 and 0·71, respectively. Among fossil forms, the closest approach to the proportion seen in the Makapan fragment is in the large female from Olduvai IV, with an index of 85%. A similar proportion (83%), was, however, seen in the only available female specimen of *T. gelada*. Although their relative depth at M_2 is similar, the shape of the corpus is rather different in the modern and the Olduvai IV form. In the Bed IV female, the inferior margin of the corpus is approximately parallel to the occlusal plane in the molar region, thus resembling the lighter-jawed Kanjera and Olorgesailie females. In *T. gelada* the inferior border diverges anteriorly from the occlusal plane, the corpus attaining its greatest depth below M_1. The Makapan female fragment is too incomplete for either of these shapes to be discerned, although it can be seen that its depth was greater below M_2 than M_1. In the male fragment M 626, however, the full depth of the corpus is preserved below M_3 and M_2, and the inferior border and the occlusal plane can be seen to diverge anteriorly quite strongly in this region. Thus, although the corpus is not fully preserved at the level of M_1, it can be presumed to have been considerably deeper than at the level of M_3. A similar shape is distinctive of males of *T. gelada*, but is not seen in Olorgesailie males, or the probable male fragment from Kanjera (M 11541), in which the inferior border of the mandible runs more or less parallel to the occlusal surface in the molar region, just as in females from these sites.

Teeth

These have been fully described and figured by Freedman (1957, 1960). Casts of some of Freedman's specimens were examined (M 2974, M 2967, M 2991, M 626, M 533). The molars, first described by Freedman, show the characteristics of the genus: accentuated fossae and clefts and marked asymmetrical hypsodonty. In a number of ways, however, they differ from those of the Kanjera form. In the upper molars the median lingual cleft is less well-developed, and V-shaped rather than rectangular in occlusal aspect, so that the lingual cusps are less well-defined columns. In the M^3 of M 2967 (Fig. 15 in Freedman, 1960), the mesial lingual cleft appears to have been, even in the unworn crown, relatively weakly developed. The whole buccal face of the tooth is very flat, with little of the columnar bulging of the buccal cusps typical of the genus. The medial buccal notch is a more open 'V', relatively shallow, especially as compared with the lingual notch.

Complementary differences are to be seen in the lower molars. As compared to Kanjera, the median lingual notch is less deep relative to cusp height, and is without 'beading' along its lingual margin. Because the talonid basin and distal fovea are less extensive, the entoconid is relatively larger, more conical and less columnar. The lingual margin, especially on the entoconid, is sharper. The median buccal cleft is not defined by a ridge, so that its floor is more continuous with the buccal face. In the M_3, the distal buccal notch is a more open 'V' than in the Kanjera form, and the distal fovea is smaller relative to the hypoconulid.

While these molar characteristics are not easily quantified, and each one is comparatively minor by itself, in sum they produce a tooth which is distinctly closer to the typical cercopithecine condition than is that of the Kanjera form, and which possibly may be considered more primitive.

The premolars do not appear to differ from those of the typical form, except that the sectorial face of the male P_3 is considerably more elongated relative to its breadth and to general dental size. This suggests that the upper canine of the Makapan form was more high-crowned than that of Kanjera, a prediction confirmed by the isolated, upper, male canine (M 2974), figured by Freedman (1960, Fig. 15) and attributed by him to *S. darti*. Although the specimen is worn, its height is still considerably greater than that of the virtually unworn Kanjera male specimen, and those from Olorgesailie. Its distal flange is also distinctly more prominent, producing a more bladelike form, which is honed to a sharp edge in its apical part. These characteristics of the canine-P_3 complex again approach *T. gelada* and the other large, living cercopithecines. On the other hand, the lower incisal region of M 626 is narrow, demonstrating as great a degree of incisal reduction as in the East African forms.

A final point of difference involves the wear on the molars. As noted, in Kanjera, Olduvai II, and Olorgesailie populations, individuals in which the third molar is erupting or in early occlusion invariably show severe wear on M_1 and a considerably worn M_2, producing a wear gradient from M_1 to M_3 which is more pronounced than in living Cercopithecinae. In the Makapan male (M 626) M_3 shows moderate wear, and had evidently been in occlusion for some time before death, but M_2 and M_1 show only moderate wear. In the Olduvai II female M 14953, by comparison, M_3 is erupting, M_2 is slightly less worn than the corresponding tooth in M 626, but M_1 is considerably *more* worn.

I. SWARTKRANS

Swartkrans, one of the cluster of early Pleistocene localities in the Sterkfontein valley, near Krugersdorp, Transvaal, has been described by Robinson (1952) and Brain (1958, 1970). The fossiliferous deposit, like the others in the district, consists of the cemented infilling of a cavern in dolomitic limestone, itself the result of subterranean solution.

The *Theropithecus* material from the site was extensively described and figured by Freedman (1957). All the described material is cranial and dental: a pelvis is mentioned by Freedman, but not described, and might equally well be attributed to *Dinopithecus ingens.*

About twenty specimens comprise the hypodigm, including a muzzle, some mandibular fragments and a crushed skull, all of females, and some male mandibular fragments.

From Freedman's description the Swartkrans form resembles the East African in most cranial characteristics; mandibular fossae are absent, the incisal region narrow and the temporal lines (in the female, and by implication in males also) meet well forward on the cranial vault. However, one at least of the Swartkrans females has a muzzle that is considerably higher anteriorly than those of the East African forms, and bears a deep maxillary fossa (Freedman, 1960). On the other hand, another Swartkrans female has no maxillary fossa, agreeing with the East African forms. As this feature is not generally so variable within populations of living Cercopithecoidea, the question arises of whether more than one form of *Simopithecus* occurs at Swartkrans. If this were so, they need not necessarily have been synchronic, since the filling of the cave is believed by some to have occupied a considerable space of time (Wolpoff, 1968).

The cheek teeth of the Swartkrans form do not differ significantly from the Kanjera sample in structure, and those specimens which were examined as casts do not show the supposedly primitive features seen in the Makapan teeth. The male P_3, however, is relatively longer than that of Kanjera, though not as extreme as in the Makapan male.

J. HOPEFIELD

This open site situated off the arid western coast of Cape Province has been described by Singer (1962) and Singer and Keen (1955) and Keen and Singer (1956). The specimens, described in detail by Singer (1962), comprise a cranial vault, probably female, a number of cheek-teeth associated with a female P_3 and canine, a fragment of the posterior part of a massive mandible, several isolated teeth, and the proximal end of a radius.

The morphology of the cranial fragment agrees closely with that of Kanjera females, including such generically diagnostic features as the long and massive postglenoid process, and the narrow postorbital constriction. The corpus of the fragmentary mandible, though large and massive, is not deep.

The total range of dental size represented by the sample is considerable. While the smallest teeth and the cranium are comparable to females of the Kanjera form, the teeth of the large fragment can be matched only among males of the Olorgesailie and Olduvai IV samples. It is questionable whether such a range can be attributed solely to sexual dimorphism and intra-populational variability, and the possibility arises that more than one form may be represented, a possibility which can only be tested in the light of further material.

III. THE AGE OF THE *SIMOPITHECUS* SITES

The traditional framework for dating fossil sites in tropical Africa, the sequence of 'pluvial' and 'interpluvial' periods, believed to be correlated with the glacial and interglacial periods of higher latitudes, has been severely shaken by recent reappraisals (Flint, 1959). Although it is clear that climatic fluctuations have occurred widely in the African Pleistocene, it is quite uncertain how many such episodes should be recognized, whether they were synchronous throughout the region, and how far they can be related to glacial events.

Recent advances in geochronology are rapidly replacing the glacial-pluvial timescale with one based upon chronometric dates. While some of the *Simopithecus* sites can be situated directly on this scale, most must still be related to it on faunal, cultural and stratigraphical evidence.

The whole of the main Olduvai series was referred by Hopwood (1936, 1951, etc.) to the Middle Pleistocene. With better faunal evidence, however, it has become apparent that the deposits cover a very extensive period of the Pleistocene, a conclusion supported by the K-Ar dates of about 1·8 and 1·7 million years for the basal basalt and *Zinjanthropus* horizon of Bed I respectively. (Leakey, Curtis and Evernden, 1961; Hay, 1963). The length of the hiatus thought to occur within Bed II is unknown, although a Potassium-Argon determination from the lower part of the bed, below a prominent series of aeolian deposits, yields a date of 1·1 million years B.P. (Hay, 1963). Recent evidence from magnetic reversals suggests that the lower part of Bed IV may be as old as 700,000 years. In this case, the sites such as BKII in upper Bed II may be closer to one million years than to half a million as has been supposed (Grommé and Hay, 1971; M. D. Leakey, 1971). Bishop (1963) points out that a lengthy period of volcanic quiescence is indicated by the laterisation of hill-slope soils later incorporated into Bed III. How far this period is represented in the Olduvai sequence as a depositional gap is not known. On cultural grounds, the latest levels of Bed IV are unlikely to be older than 60,000 years, while the lower layers may be as old as 700,000 years.

The Kanjera deposits were dated by Leakey (1950) to the Kanjeran pluvial, which was named after them. This was correlated with the Riss glaciation of the European sequence, antedating 100,000 years B.P. (Oakley, 1966). Among East African sites he correlates Kanjera with the lower part of Bed IV, Olduvai. Oakley (1966) would, however, date Kanjera to about 60,000 years B.P., presumably largely on cultural grounds. The fauna, especially the elephantids (Maglio, pers. comm.) supports a general equivalence in age between Kanjera, Olorgesailie, and Olduvai Bed IV.

The Olorgesailie beds can be tied tentatively to the Olduvai sequence on cultural grounds. The human culture (Isaac, 1966b) is considered by Howell and Clark (1963) to be close to Chelles-Acheul 9, the third of five hand-axe culture stages occurring within Olduvai IV. Howell (1967) charts the Olorgesailie beds as spanning a time interval from 200,000 to 75,000 years B.P. The *Simopithecus* material is derived from a land surface approximately in the middle of the vertical sequence, and may thus be dated to about 120–100,000 years ago. The single radiometric date from the site (0·5 million years from an included, water-borne pumice) is unexpectedly high, and derivation from earlier deposits is suspected (Curtis, 1967). It is, however, consistent with the new evidence for the age of Bed IV, Olduvai, cited above.

Both Leakey (1943b) and Arambourg (1947) dated the Omo deposits to the earliest Pleistocene, antedating Olduvai. Leakey (1963) considered Olduvai I at least partly contemporary with the Omo beds, as did Cooke (1963). The recent Omo Research Expeditions (Howell, 1969, Butzer and Thurber, 1969); have broadly confirmed these conclusions, while greatly clarifying the stratigraphy of the Omo basin deposits and providing a series of radiometric dates. These show that the Omo beds of the earlier expeditions, now known as the Shunguru, Usno, Nkalabong and Mursi formations (Butzer and Thurber, 1969), do indeed immediately antedate Olduvai I, spanning a period from about 1·8 million years B.P. to an indeterminate base antedating 4·25 million years.

Early interpretations of the stratigraphical evidence which attributed the Kaiso fossiliferous beds to an interpluvial (Wayland, 1926), specifically the 'Kanjera-Kamasian' (Leakey, 1951), have been plausibly disputed (Flint, 1959, Bishop, 1968). Fuller investigations have shown the formation to be considerably thicker than anticipated, and perhaps to span several million years (Bishop, 1968). Faunal evidence, which has long led to the conclusion that formation as a whole was early in the 'Villafranchian' sequence (Leakey, 1951, Cooke, 1963) now suggests that it may have been deposited almost entirely within the Pliocene as currently defined, between about 5 and 2 million years B.P. (Bishop, 1968, Maglio, 1970).

The relative and absolute ages of the South African australopithecine cave breccias have been variously interpreted on petrological, faunal and stratigraphic evidence, and are still hotly debated. King (1951) attributed all the sites to a single depositional cycle, relying on geological evidence which Robinson (1952) and Brain (1958) showed to be misinterpreted. Brain's petrological studies led him to the conclusion (disputed, however, by Butzer (1970)) that breccias at neighbouring sites in the Sterkfontein valley were accumulated under different climatic conditions and therefore could not be contemporary, while the faunal evidence also suggests a long total span for the breccias (Robinson, 1952). Inferences about the sequence of formation of the breccias which were drawn on the grounds of correlation with the supposed pluvial-interpluvial sequence (Oakley, 1954a; Brain 1958), are no longer valid (Flint, 1959). While interpretations of the faunal evidence differ in detail (Oakley, 1954a; Howell, 1963), there appears to be general agreement with Cooke's (1963, 1968) position that they can be grouped into an early span which includes Makapan, and a later one including Swartkrans.

The dating of the breccias relative to sites elsewhere in Africa and to the chronometric scale presents peculiar problems (Tobias and Hughes, 1969), and at present relies almost entirely on faunal evidence. At one extreme the whole group has been assigned to the Middle Pleistocene (Kurtén, 1957), at the other, to the Upper or even Middle Pliocene (Broom, 1945; King, 1951; Robinson, 1952). Most authors appear to accept that the deposits are, as a group, of 'Villafranchian' age (e.g. Oakley, 1954a, 1966; Ewer, 1956; Brain, 1958; Howell, 1963; Cooke, 1963) however, recent chronometric determinations have shown that this supposed stage in Africa in fact includes faunas of a wide variety of Plio-Pleistocene ages. Cooke (1968) in a review of the faunal evidence suggests a broad equivalence between Swartkrans and Olduvai lower Bed II, which would suggest a date between two and one million years. Makapan is included in his 'Sterkfontein Faunal Span' which, however, includes sites now thought to range from about 1·5 million years (Olduvai I) to more than four million years (Kaiso). Furthermore, material from the still earlier sites of the Eastern Rift was not available for comparison at the time at which Cooke completed his revision. On present evidence it would seem that the breccias of the Sterkfontein Span might be distributed anywhere between five and two million years. A long and generally early timescale for the australopithecine breccias seems most plausible, and in the absence of chronometric dates is not contra-indicated by the high K-Ar date of Olduvai Bed I, as Leakey, 1963, seems to suggest.

Hopefield is rather securely dated, on faunal and cultural grounds, to the late Middle or early Upper Pleistocene (Singer et al, 1955; Cooke, 1963, 1968), later than Olorgesailie and Kanjera, and probably equivalent to, or rather later than, the latest layers of Bed IV Olduvai, with a chronometric date of about 50,000 years B.P. (Oakley, 1966).

The Koobi Fora site is reliably dated at close to 2·6 million years by K/Ar determination (Fitch and Miller, 1970). Ternifine is generally agreed to date from the

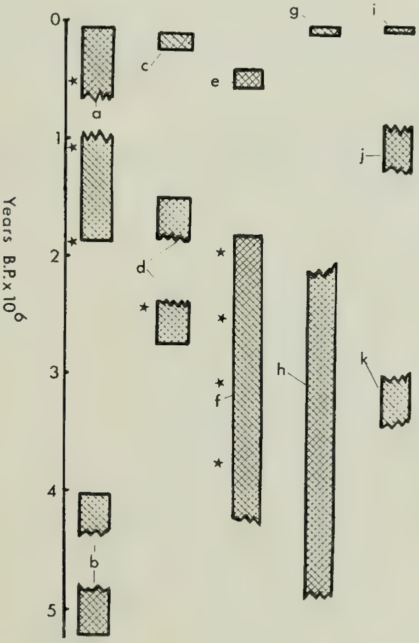


FIG. 17. Tentative chronological correlation of *Simopithecus* sites. a. Olduvai. b. Lothagam. c. Olorgesailie. d. East Rudolf. e. Ternifine. f. Omo. g. Kanjera. h. Kaiso. i. Hopefield. j. Swartkrans. k. Makapan. Stars indicate Potassium-Argon Age determinations. Note: Discoveries made since this diagram was prepared suggest that the Olduvai 'Upper' series is probably older than represented here, perhaps ranging from 1 to 0·4 million years B.P. (M. D. Leakey, 1971). By implication, Olorgesailie is also older than represented.

Middle Pleistocene, with a general equivalence in date to late Olduvai II, III or early IV. (Cooke, 1968). A suggested, tentative, correlation of sites with *Simopithecus* is shown in Fig. 17.

IV. THE SIZE OF *SIMOPITHECUS*

Simopithecus frequently appears in the literature as a 'giant baboon', while other authors have emphasized that the type (Kanjera) population consisted of animals no larger in body-size than some living baboons. Reliable evidence of body-size (derived from the post-cranial skeleton) is only available for the Kanjera and Olorgesailie populations. Using the results obtained on these series, it is possible to estimate the body-size of the remaining series on the basis of their jaw size.

Stature can be estimated within broad limits from the lengths of the long-bones. In the Kanjera form, these values are close to those seen in *Papio anubis neumanni* of similar sex. This is the living baboon of the Kenya Rift and Serengeti areas, and is slightly smaller than the typical *P. anubis* (Jolly, 1965).

The Olorgesailie form was obviously much larger than any living cercopithecoid. In the male, the humerus and femur (tibial and radial length are unknown) are comparable in length to those of chimpanzees or small female gorillas. In females they are shorter, roughly comparable to males of large forms of *Papio*, although the femur is relatively shorter than in that genus.

Body-weight was estimated on the basis of the hypothesis that it would be roughly proportional to the cross-sectional area of the humerus and femur, through which the weight is transmitted from the body to the ground in the quadrupedal stance. An expression of humeral and femoral cross-sectional area ('robusticity quotient') was derived by the formula (humerus shaft transverse breadth + anterior-posterior breadth)^2 + (femur shaft transverse breadth + anterior-posterior breadth)^2. Breadths were measured on the humerus at the level of the midpoint of the insertion of M. teres major, and on the femur approximately midway between the lesser trochanter and the distal end of the diaphysis. This value was calculated in several series of skeletons of extant Anthropoidea (*Papio*, *Mandrillus sphinx*). Ideally, values of the robusticity quotient should have been plotted against body-weight in a number of individual specimens weighed at the time of collection, but very few of these were available. A mean value of the expression was therefore calculated for each of the series, and plotted against a mean weight for the species derived from published sources (Snow, 1967, for *P. anubis*; Malbrant and Maclatchy, 1949, for *M. sphinx*). The regression so obtained is approximately linear (Fig. 18). The Kanjera and Olorgesailie limb-bone dimensions are projected on to the regression to yield an estimate of body-weight. Kanjera females are the smallest, with a body-weight in the neighbourhood of 20 kg, close to males of *T. gelada*. Kanjera males weighed about 35 kg, about the same as males of the largest extant forms of *Papio*. Olorgesailie males, however, probably weighed in the neighbourhood of 65 kg, as large as a female gorilla. In spite of this impressive size, however, they were far below the bulk of the male gorilla, which weighs at least 140 kg.

The body-size of the remaining series can be estimated only from the size of their jaws and teeth. An index of cheek-tooth area was therefore made for each of the *Theropithecus* samples by summating the products of the average length and breadth of P_4, M_1, M_2 and M_3. The regression of points derived from plotting these values against the weight of males as estimated from limb-bone cross-sectional area is approximately linear. Points derived from the series for which no limb-bones are available can then be projected on to the regression, to derive the estimates listed in Table 11. Needless to say, weights estimated in this way are subject to wide margins of errror, and can be regarded as approximations only. Nevertheless it is possible to state that the smallest Pleistocene *Theropithecus* was larger than the living gelada, and approached the largest living baboons in size, while the largest of them was a giant among Cercopithecoidea, as bulky as a small gorilla. Even the latter, however, was far less massive than male gorillas and, it may be surmised, than *Gigantopithecus*, which remain the largest primates known.

V. PHYLOGENY AND TAXONOMY

A. Intrageneric Diversity

The major parameters of variation observed between between fossil populations attributed to *Theropithecus* include absolute size, dental proportions and morphology, and facial and cranial shape. Unfortunately, not all of these can be documented in each sample.

Of the series described in the previous sections, Olorgesailie and Kanjera may probably each be considered as a sample drawn from a synchronous population.

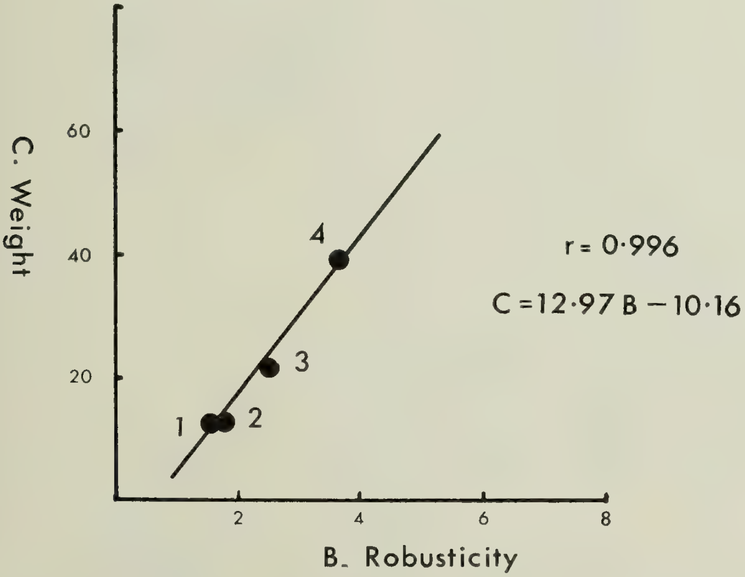


Fig. 18. Mean weight plotted against mean Robusticity Quotient in *P. anubis neumanni* males (point 3) and females (2), and *Mandrillus sphinx* males (4) and females (1).

TABLE II

Estimates of mean body-weight in *Theropithecus* populations, and data from which these were calculated

Form	A. Molar Area Quotient		B. Robusticity Quotient		C. Body-weight	
	Value (cm²)	Source	Value	Source	Value (Kg.)	Source
P. anubis neumanni, male	—	—	2·52	Mean of 2, USNM + AMNH	21·75 ± 2·18	Snow, 1967 (N = 10)
,, ,, female	—	—	1·82	Mean of 3, AMNH + BMNH	12·32 ± 1·24	,, ,,
Mandrillus sphinx, male	—	—	3·76	Mean of 3, AMNH	39	Malbrant, Maclatchy, 1949
,, ,, female	—	—	1·596	Mean of 3, AMNH	12	
T. gelada, male	4·10	Mean of 8, (AMNH + BMNH 24.8.7.5).	2·065	Mean of 2	16·62	Estimate from B
Kanjera male	7·10	Kanjera series	3·46	Kanjera series	34·72	Estimate from B
Kanjera female	5·90	,, ,,	2·39	,, ,,	20·84	,, ,,
Olorgesailie male	11·47	Olorg. series	5·63	Olorg. series	62·86	,, ,,
Makapan male	6·69	Makapan series	—	—	32·79	Estimate from A
Swartkrans male	9·36	Swartk. series	—	—	49·58	,, ,,
Olduvai IV male	11·88	M 14680	—	—	65·42	,, ,,

The Makapan and Swartkrans series were treated in a similar way, in the absence of evidence that the time-span during which they accumulated, while undoubtedly considerable, was significant against the scale of mammalian evolution. This view is not unchallenged (Wolpoff, 1970), and might be disputed on the grounds of the considerable range of variation in size and structure documented for both sites by Freedman (1957). Some of the Olduvai sub-series are related to a single site (such as BK II), and probably sample single synchronous populations. Others consist of specimens which are known to be broadly equivalent in age but cannot be treated as truly synchronic (e.g. the two specimens from Bed IV). The remaining series (Kaiso, Arambourg's Omo specimens, and the published Hopefield material) are too small and fragmentary to contribute significantly to establishing the evolutionary framework of the genus.

Previous authors have commented on the wide variation in absolute size within the genus. The size of the postcranial remains of Kanjera and Olorgesailie shows quite clearly that the latter was much the larger of the two. In the few cases where individual specimens of the series overlap this can be attributed to immaturity in the Olorgesailie specimen. Whereas the Kanjera animal was about the same size as the living chacma baboon (the largest form of living *Papio*), the Olorgesailie form was much larger than any living cercopithecoid (see section IV).

The same relationship is seen in cranial size. The juvenile frontal fragments from Olorgesailie are as large or larger than the equivalent parts in mature Kanjera males.

The few comparable cranial dimensions suggest that the Swartkrans form was somewhat larger than Kanjera, while Makapan was a little smaller.

These size-relationships are borne out by dimensions of the cheek-teeth (Table 4). In all but a few cases the smallest specimens of the pooled Olorgesailie series (which must be female) are larger than the biggest Kanjera males. Exceptions are the breadth of P^3 which is apparently as great in Kanjera as in Olorgesailie males, and the length and breadth of the female P_3, which is much the same in both samples.

Ranges of tooth-size in the Swartkrans, Kanjera and Makapan series overlap broadly, but suggest that Swartkrans was larger, and Makapan smaller, than Kanjera. Swartkrans dimensions overlap with those of Olorgesailie in such a way as to suggest that females of the East African form were about equivalent in size to males of the South African. Makapan overlaps with Olorgesailie only in P_4 breadth. The form from Bed I, Olduvai, is closely comparable to Swartkrans in dental size, but the upper Bed II form is larger, approaching Olorgesailie. Bed IV is larger still. The Omo material probably represents both sexes of a form about the same size as Swartkrans or Olduvai I. The Kaiso teeth might, by their size, have belonged to the Makapan form. As described earlier, the dimension of the Hopefield specimens suggest that two forms were represented in the sample, one about the size of Swartkrans, the other at least as large as Olorgesailie.

Statistical comparison of means of cheek-tooth dimensions is of limited value, since samples of teeth that could be realiably sexed were small, and reliable sexing is obviously a prerequisite of any statistical technique which involves the assumption that the sample is unimodally distributed. However, a few significant results were obtained using Student's t-test with Bessel's correction for small samples (Moroney, 1956). The mean of P^4 breadth is greater in Kanjera than in Makapan females, that of M_2 anterior and posterior breadth is greater in Swartkrans than in Kanjera females. In Makapan males the P_3 is significantly narrower than in Olorgesailie males, but both the South African forms had male P_3s that are significantly *longer* than those of the much larger Olorgesailie male. This expresses the difference between them in dental proportions.

Figs 10 and 11 show diagrammatically the means of tooth-dimensions in each sex and the four series. Both males and females show the order of increasing dental size Makapan-Kanjera-Swartkrans-Olorgesailie.

These observations suggest a general trend towards increasing size through the known history of the group, in so far as the earlier are the smallest, while 'giant' forms appear at the end of the sequence. However, the Kanjera series is both small and apparently late.

All the populations show the characteristic, complex and high-cusped cheek-teeth described above for Kanjera. However, there is interpopulational variation in the degree to which these characteristics are expressed. The large, late populations show greater crown complexity than the typical form, but this may in part be a size-related effect. The converse characteristics in the Makapan form, however, are probably truly primitive, and serve to link the genus with more typical Cercopithecinae. The most notable inter-populational variation in dental proportions is seen in the canines and anterior lower premolar of males. In the South African forms these teeth resemble their homologues in *Papio* males; the canines are high-cusped and blade-like, and the P_3 has a long, sectorial, mesio-buccal face. The canine-P_3 complex is especially large, relative to the rest of the cheek-teeth in Makapan males.

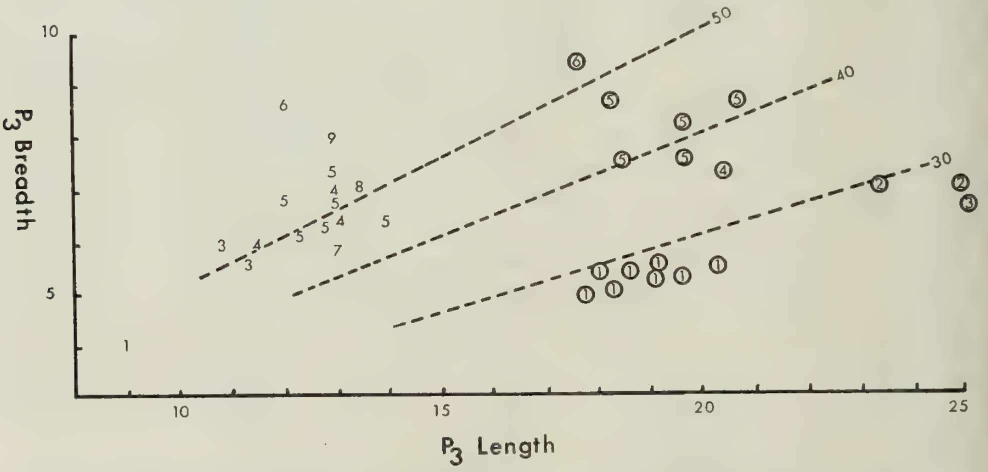


FIG. 19. Lower third premolar shape in *Theropithecus*. Breadth plotted against length with selected percentiles of Breadth/Length index. 1. *T. gelada*. 2. Swartkrans. 3. Makapan. 4. Kanjera. 5. Olorgesailie. 6. Olduvai IV. 7. Olduvai II. Males ringed, females unringed.

In Olorgesailie males the P_3 is strikingly short in comparison with its breadth (Fig. 20) and with the size of the cheek-teeth posterior to it (Fig. 10). Its shortness is due to a reduction in its mesio-buccal face, which in turn can be related to modifications in the upper canines, which are comparatively low-crowned and more circular in cross-section than those of a typical cercopithecoid. The Kanjera male, so far as can be judged from the rather small available sample, showed P_3 proportions and a canine size and shape intermediate between those of Olorgesailie and the South African forms (Fig. 19). The type of *S. leakeyi* Hopwood from Bed IV, Olduvai has an even shorter and broader P_3, and the tooth is as yet unknown in the other populations.

Fig. 20 shows the mean length of the male P_3 in the various fossil samples expressed by plotting it against the total length of the molars. There is a clear tendency for P_3 to become relatively shorter and broader in the later forms; its length is 50% of molar row length in Makapan, 45% in Swartkrans, between 30 and 35% in Olorgesailie, and less than 30% in the latest form, Olduvai IV. An apparent discrepancy is seen in the Kanjera form, which is closer to Swartkrans in proportions than to its supposed near contemporaries, Olorgesailie and Olduvai IV. The explanation might be that Kanjera is a primitive survival, or that the date of the site is earlier than generally believed. On the other hand, the fact that it was a much smaller animal than Olorgesailie and Olduvai IV suggests that its apparently primitive proportions might be due to allomorphosis. Such an effect is apparent in the P_3/molar relationship in extant *Papio*. As shown in Fig. 21, when mean length of P_3 is plotted against molar length, there are considerable inter-populational variations in proportions. Thus, male P_3 length in the very small baboon *Papio cynocephalus kindae* is about 45% of molar row length while in the large *P. ursinus* it exceeds 60%. However, as all points lie close to a straight line, the implication is that animals of all populations are affected by a single differential growth constant, the differences in proportion being due solely to variation in the length of the developmental span during which the growth constant is expressed in forms of different absolute size. (Freedman (1962b) found a similar relationship between calvaria length and facial length in *Papio*). The differential growth constant postulated for fossil *Theropithecus* is, of course, opposite in direction, with absolutely *smaller* forms having relatively longer P_3 and larger canine. As in *Papio*, however, the larger forms would show the apparently more specialized, and smaller ones the more primitive condition. A further implication of this hypothesis is that the differential growth constant itself was modified during the course of the evolution of the genus from a condition perhaps not unlike that seen in *Papio* to that seen in the advanced Pleistocene *Theropithecus*. This explanation of variability in the relative size of the canine-P_3 complex must be regarded as hypothetical pending the description of series of synchronic populations of different absolute size from time-levels other than the Middle Pleistocene.

The indications are that the shape of the skull, especially the facial part, showed considerably more inter-populational variation in fossil *Theropithecus* than did the structure of the teeth (cf. Ewer (1956) for a similar situation in fossil pigs). The Swartkrans form (or, perhaps, one of them if more than one is present) is distinguished from Kanjera, Olorgesailie, and Olduvai II by the relatively great height of the

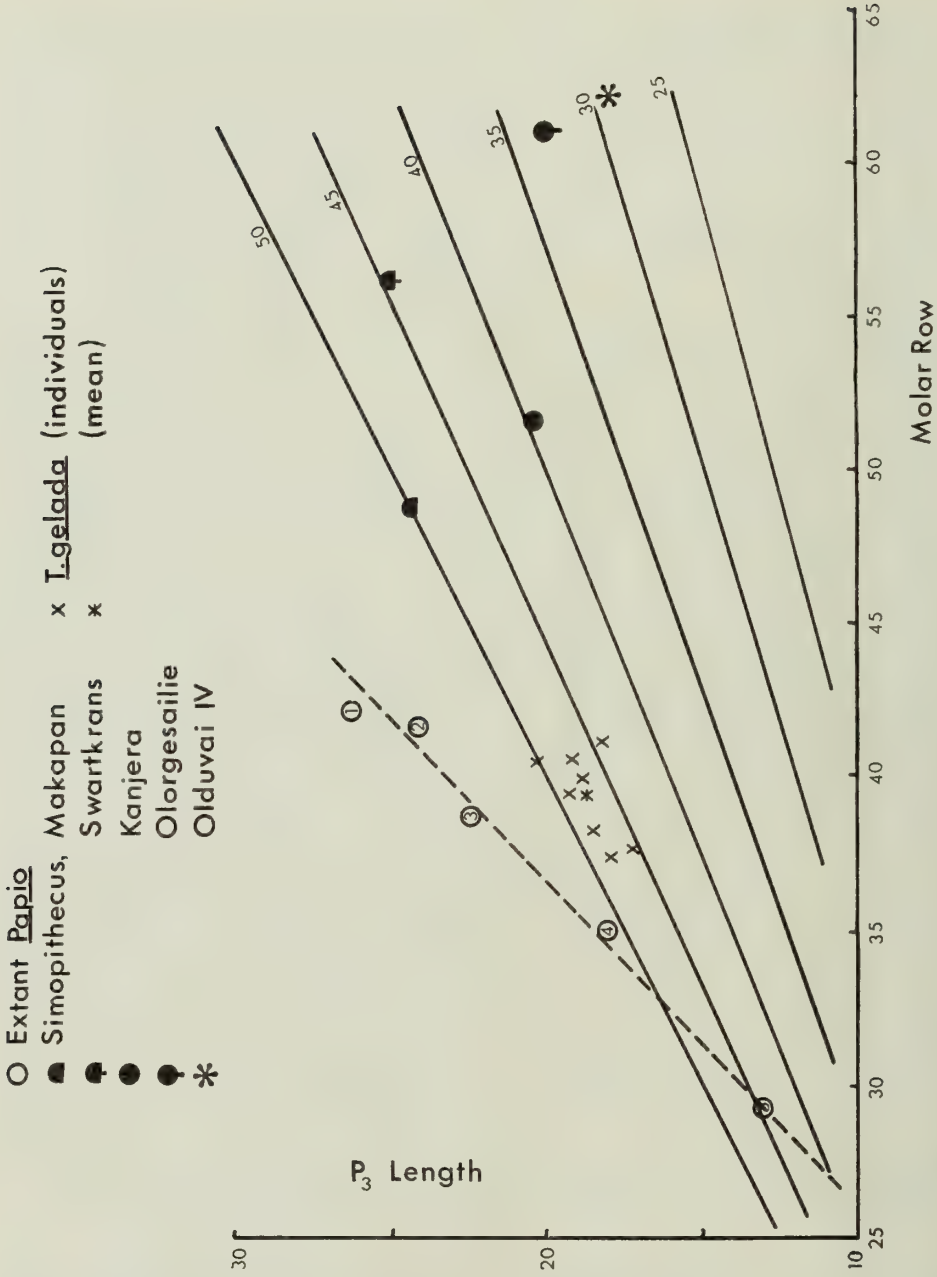


FIG. 20. Relative length of P_3 in males of *Theropithecus* and *Papio*. Mean P_3 length plotted against sum of mean lengths of three molars. Regression for *Papio* fitted by eye. (M_3 of Olduvai male is unknown; its length is estimated from the length of the female M_3).

anterior part of the muzzle (in females, at least) and by the occurrence of a maxillary fossa. Unfortunately the appropriate parts are absent from the other samples.

TABLE 12

Expressions of the relative height of the anterior muzzle in female *Theropithecus*

a = Height of muzzle anterior to third premolar
b = Length P^3 + Length P^4
c = Length M^1 + Length M^2

	a (mm)	b (mm)	c (mm)	$\frac{100b}{a}$	$\frac{100c}{a}$	$\frac{100b}{c}$
Swartkrans SK 563	46	16·0	28·6	34·8	62·2	55·9
Olduvai II M 18779	25·1	18·1	—	72·1	—	—
Kanjera M 14936	22	—	25·1	—	114·1	—
M 11537	20	14·1	25·1	70·5	125·5	56·2
T. gelada BM 24.8.7.5	14·2	10·6	20·4*	74·6	143·7	51·9

*Estimated, since M^1 absent

Mandibular fossae are known to be absent in Swartkrans, Olduvai II, Kanjera, Olorgesailie and Olduvai IV, and in some individuals of the Makapan sample. The male specimen (M 626) from Makapan, however, has an extremely deep fossa. The Olduvai I female has a slight fossa which probably indicates that the male of the form had a rather deeper one. The indications are therefore, that the possession of a fossa was a primitive character for the genus which was lost during the course of its evolution. In each of the later forms (Kanjera, Olorgesailie, Olduvai II, Olduvai IV) the internal profile of the symphysis is flat and scarcely excavated. Makapan again differs in showing a steeply-sloping symphysis, and Olduvai I is probably intermediate. The lateral profile of the mandibular corpus, more or less parallel-sided in the later forms, broadening from M_3 forwards in Makapan and to a lesser extent Olduvai I, shows, similar pattern of variation over time, and is perhaps related functionally and genetically to the last.

All the populations of fossil *Theropithecus*, apart from those represented by very small and incomplete samples, can thus be separated from one another on the grounds of size, or shape, or both. In translating this pattern of variation into the most likely phyletic tree connecting them over time we must bear in mind the likelihood of considerable polytypic variation, especially in size, within single species of widespread, terrestrial Cercopithecoidea, analogous to that seen in *Papio* (Jolly, 1965; Jolly and Groves, in preparation). Thus, unless populations differing in size and size-related characters can be shown to be strictly sympatric and synchronic we should hesitate to use their existence as evidence for the occurrence of cladogenesis. With few exceptions, the data are consistent with the view that all of the samples are representative of a single, polytypic but anagenetic phylum becoming progressively specialised over the course of its evolution.

There seems little reason to doubt that the Makapan *Theropithecus* was primitive, and could have been ancestral to later forms. The co-existence of different morphological types in the sample could be interpreted in several ways; it perhaps indicates a variable population which was in the process of losing the mandibular fossa, possibly it includes a mixture of specimens of different ages, representative of different populations along a chronocline, or, as a third possibility, it includes representatives of two synchronic species, rather similar in size, one of which retained primitive characteristics while the other was moving in the direction of later forms like Kanjera. While the third of the possibilities seems the most likely, one would not, without having examined the original material, insist on it in opposition to Freedman's view that all Makapan *Theropithecus* can be assigned to a single species.

The Olduvai I form, though imperfectly known, can be plausibly seen as a somewhat larger, more evolved descendant of Makapan, and Omo might well be similar. The Swartkrans sample again shows resemblances to Olduvai I in absolute size, and, although homologous parts are not available for comparison, seems to have departed to the same degree from the primitive condition seen in Makapan. It thus seems reasonable to assign all of them to different populations of a single lineage Further information is needed, however, especially about the height of the female muzzle, the occurrence of facial fossae, and the size of the male canine-P_3 complex in Olduvai I and the profile of the mandibular symphysis in Swartkrans.

There is little reason to question the derivation of the Olduvai II form from one resembling the Olduvai I and Swartkrans form. Equally there is nothing in its structure, as known at present, to disqualify it from a position ancestral to the Kanjera, Olorgesailie and Olduvai IV forms.

If Kanjera and Olorgesailie are truly contemporary, the question arises whether the considerable difference between them implies that they belonged to separate synchronic species. While a case could be made for specific separation, the view is here adopted that they more probably represent populations within a single, polytypic species. This interpretation is supported by the existence of considerable variation in size and size-correlated characteristics among populations of contemporary *Papio* which are not fully isolated genetically from one another.

Both in size and dental morphology, the juvenile fragment from Bed IV is appropriate to a more specialized population descended from Kanjera-Olorgesailie. The type of *Simopithecus jonathani* is clearly also a specialized representative of the genus, but its relationship to the previous specimen poses some problems. If it is indeed a female, as has been commonly supposed, then its general size suggests that it was drawn from the same population as the juvenile male, but its relatively large canine would indicate a completely new evolutionary trend not foreshadowed in any other population of the genus. If, on the other hand, it is a male, then its smaller size and extremely 'feminised' P_3 separate it from the juvenile male. There is apparently a possibility (R. E. Leakey, pers. comm.) that the *jonathani* jaw was derived from a gully-filling within Bed IV, and therefore dates from the extreme end of the main Olduvai sequence. If this is so, then it could be seen as representative of a very late, specialized population derived from that represented by the juvenile jaw.

The question of the coexistence of separate species of *Theropithecus* during the deposition of Olduvai IV will only be resolved with the description of new material precisely localized within the deposit.

It has long been recognized that the gelada baboon is the closest living relative of *Simopithecus* (Andrews, 1916). It shows, to some degree at least, all the distinctive features seen in the fossil forms: the large, high-crowned and complex cheek-teeth, the relatively small incisors, the relatively high and vertically orientated mandibular ramus, the forwardly-set temporal musculature, the high face with deep posterior maxilla, and the postcranial characteristics associated with extreme terrestrialism. While it is possible that the gelada has acquired these characteristics by parallelism, a view which is supported by the fact that they seem to comprise a single functional pattern (see below), the more economical hypothesis would seem to be that they are truly homologous. On the other hand, it seems unlikely that *T. gelada* is derived directly from *Simopithecus* of the Middle to Upper Pleistocene, from which it differs in having somewhat less specialized molar crowns (in particular, the trigon and talonid basins are less deeply excavated, so that the 'median longitudinal ridge' is a less prominent feature in the worn tooth), unreduced male canines and P_3, deep maxillary and mandibular fossae (the latter especially in males), a hollowed-out internal symphyseal profile, and a mandibular corpus which deepens towards the symphysis, again especially in males. In each of these characteristics the gelada resembles the condition believed to be primitive for the *Simopithecus* line, seen especially in the Makapan material, and progressively lost in later populations. Some of the apparent primitiveness of *T. gelada* may be due to its small size; for example, if our hypothesis about allomorphic influences upon relative canine size is correct, then a small form at any evolutionary stage would have had a relatively large male canine-P_3 complex. This is not, however, true of the facial fossae or the shape of the mandibular corpus and symphysis which seem more likely to be genuinely primitive. Two other features, however, ally *T. gelada* with late, rather than early *Simopithecus*. First, its anterior muzzle is even lower than that of the Kanjera form, and thus differs strongly from the early *Simopithecus*, if Swartkrans is representative of the latter. Second, its mandibular ramus is as vertically disposed and its temporal musculature as anteriorly placed, as in the later forms of Olorgesailie, Kanjera and Olduvai IV. Since the latter feature may be seen as functionally related to the dietary specialisation common to the whole genus (see below), it is not unlikely that it arose independently in *T. gelada* and the lowland forms. Other gelada characters, such as the narrow nasal aperture, the evenly concave facial profile, the pre-nasal tubercles, and the narrow, almost hemispherical premaxilla do not appear in either primitive or advanced forms of the *Simopithecus* line. The first may perhaps, as in local populations of *Homo sapiens* (Coon, 1965), be considered an adaptation to breathing the dry, cold air of high altitudes; the last may be associated with a unique gelada facial gesture – the 'lip-flip' displaying the pale, prominent mucous membrane of the premaxillary gum, and the lining of the upper lip.

The array of characteristics shown by *T. gelada* suggests that it is the result of an evolutionary line which diverged from that leading to the lowland fossil forms after the development of the basic adaptive pattern of the genus, but before the specialisation seen in the later forms had been acquired. This divergence might have occurred at any time subsequent to the differentiation of the genus, but probably was not later than Makapan times. It is not impossible that the population ancestral to

T. gelada was isolated in the Ethiopian highlands during the late Pliocene, and has never been more widespread. Certainly, all fossil material described from other regions subsequent to Makapan seems to pertain to the *Simopithecus* lineage.

Authors have differed as to the degree of taxonomic relationship appropriate to expressing the similarities and differences between the gelada and its lowland Pleistocene relations. Andrews (1916), describing *Simopithecus* on the basis of the Kanjera material, recognized its affinity to the gelada, but justified generic separation on the grounds of the length of the molars and the absence of maxillary fossae. Hopwood (1934), followed Andrews' definition. Dietrich (1942) regarded *Simopithecus* as a name uncritically applied to fossil baboons ancestral to *Papio*, and accordingly reduced it to a subgenus of the latter. His '*Papio* (*Simopithecus*)

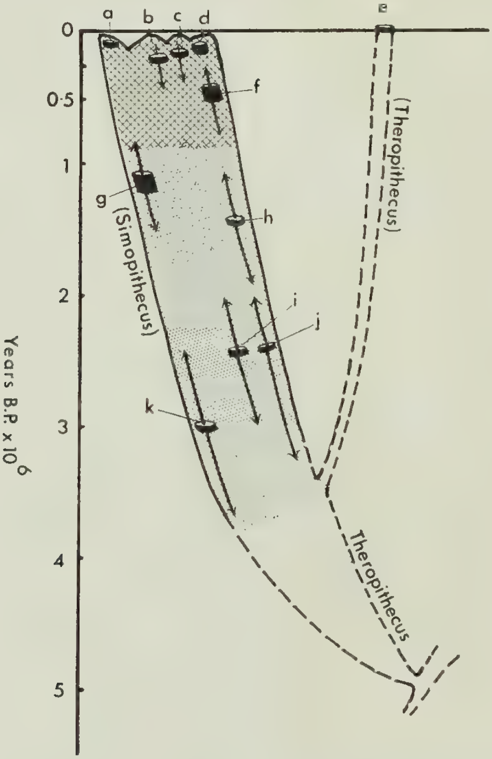


Fig. 21. Proposed evolutionary relationship of the subgenera and fossil populations of *Theropithecus*. The solid cylindrical segments represent the period of time over which each sample is believed to have accumulated. The arrows represent the probable range of possible chronological positions for each time-span. a. Hopefield. b. Olorgesailie. c. Kanjera. d. Olduvai IV. e. *T. gelada*. f. Olduvai Upper II. g. Swartkrans. h. Olduvai I. i. Kaiso. j. Omo. k. Makapan. Dotted: time-span of *T.* (*Simopithecus*) *darti*. Cross-hatched: time-span of *T.* (*Simopithecus*) *oswaldi*. Note: Information becoming available since this diagram was prepared indicates that the Olduvai, Upper II, Olduvai IV and Olorgesailie may be older than represented here. (See text.) (M. D. Leakey, 1971).

serengetensis' is however, a true *Papio* or *Parapapio*, not a *Simopithecus* or *Theropithecus*. Leakey and Whitworth (1958) list a number of dental and cranial characteristics from which they conclude that *Simopithecus* is distinct from other baboon genera, including *Theropithecus*. However, they base their diagnosis entirely upon the later, East African forms. DeVore and Washburn (1963) state flatly that '*Simopithecus* is probably *Theropithecus*', but do not justify their attribution. Most later authors (Jolly, 1966, 1967; Hill, 1970; Maier, 1970) have recognised the close relationship of *Theropithecus* and *Simopithecus* but have maintained full generic rank for each.

Almost all the diagnostic features quoted by Andrews (1916) and Leakey and Whitworth (1958) are either present also in *T. gelada*, or are absent, or variably present, in one or more *Simopithecus* populations. Apart from avoiding the difficulty of formally diagnosing *Theropithecus* and *Simopithecus* as separate genera there are major advantages to be gained from combining them in a single genus, which by priority must be called *Theropithecus*. First, it expresses the close cladistic relationship between the two lines while avoiding the necessity of groupings at the subtribal level, or of 'inflating' the whole taxonomy of the Cercopithecinae which genetically comprise a rather compact group. Second, and more importantly, it expresses, according to accepted palaeontological usage (Simpson, 1963), the fact that they share all the essential dental, gnathic and postcranial adaptive trends associated with a particular adaptive zone, unique to them among Cercopithecoidea. On the other hand, it is convenient to express in classification the hypothesis that *T. gelada* is descended from a separate branch of the genus, showing evolutionary trends rather distinct from those seen in the lineage including the known fossil forms. So long as this hypothesis holds, *T. gelada* may be classified alone in a nominate subgenus, while the known fossil forms may be assigned to subgenus (*Simopithecus*).

There is little agreement among authorities as to the number of species to be recognized in what is here defined as the subgenus *Simopithecus*. Several have been described: *S. oswaldi* Andrews 1916 from Kanjera; *S. leakeyi* Hopwood 1934 and *S. jonathani* Leakey and Whitworth 1958, both from Olduvai IV, and *S. danieli* Freedman 1957, from Swartkrans. *Papio darti*, Broom and Jensen 1946, and *Gorgopithecus wellsi*, Kitching 1953, both from Makapan, were recognized by Freedman (1957) as based upon material referable to a single species of *Simopithecus*. *Dinopithecus brumpti*, Arambourg 1947 (Omo) was also transferred to *Simopithecus* by Freedman (1957).

Freedman (1957), in the first major revision of the genus, regarded *S. oswaldi*, *S. darti* and *S. danieli* (which he proposed) as good species, defined morphologically, and later (1960) defended this view against Leakey and Whitworth (1958). The latter authors regarded the South African material, plus all that from East Africa, with the exception of the type of their new species *S. jonathani*, as representing a single species, *S. oswaldi*, within which they recognized separate subspecies, each occurring at a single site. Singer (1962) followed this scheme, suggesting that *S. jonathani* might also prove to be no more than subspecifically distinct.

The classification of the subgenus *Simopithecus* necessarily involves the arbitrary division of a continuously evolving lineage (Simpson, 1945, 1963), of which the earliest and latest representatives clearly merit specific separation. Since the Olduvai sequence is likely to provide the best time-related documentation of the evolution of the lineage at a single site, a convenient place to divide it is at a point corresponding to the depositional discontinuity in Bed II, believed to represent a general 'faunal break'. Populations preceding this break, at Olduvai and elsewhere, all show primitive characteristics and may be assigned to a single species for which the valid name is *Theropithecus* (*Simopithecus*) *darti* (Broom and Jensen, 1946), while those succeeding it can be regarded as chronologically and geographically dispersed subspecies of *T.* (*Simopithecus*) *oswaldi* In the absence of good evidence for co-existing species in Olduvai IV, *jonathani* is not accorded full specific status.

According to this scheme, the earlier species has a much larger time span than the younger. It is also much less well known; as more evidence accumulates it may well be expedient to break *T. darti* into more than one successional species.

Valid names are available for most recognizable subspecies of *T. darti* and *T. oswaldi*. If one form only is present at Makapan, it is the nominate race of *T. darti* (Broom and Jensen 1946). The type of this taxon is a male mandible lacking a fossa. If another, more primitive, form is also present, its valid *nomen* is probably *wellsi*, which was based upon the deeply-hollowed male jaw M 626. The Swartkrans form is clearly *T. darti danieli*. The early Olduvai form, considering its geographical distance, probably belonged to a separate subspecies, but cannot be diagnosed as such on present evidence, and may therefore be regarded as *T. darti* cf. *danieli*. The Omo form is also cf. *darti;* Arambourg's name *brumpti* is, however, available at the subspecific level if and when it is diagnosed, and might be applicable to the Olduvai I form also. The Kanjera subspecies is the nominate race of *oswaldi*. Leakey and Whitworth applied the subspecific name *mariae* as a *nomen nudum* to the Olorgesailie form; it is validated below (p 96) by diagnosis and the designation of a type.

The hypodigm of *leakeyi* Hopwood, 1934, was drawn from all three main 'populations' at Olduvai, (Beds I, Upper II, and IV) but its type is from Bed IV. Leakey and Whitworth used *olduvaiensis*, again without type or diagnosis, apparently as an objective synonym of *leakeyi*. There is therefore no valid name for the Olduvai II subspecies of *T. oswaldi*. No new name is proposed here, however, in view of the large amount of new material now becoming available which will enable a sounder diagnosis to be made at a later date. *Simopithecus jonathani*, Leakey and Whitworth, 1958 is provisionally treated as not separable from *T. oswaldi leakeyi*, on the conservative hypothesis that the type specimen is female. *S. oswaldi hopefieldensis* Singer 1962, based on the Hopefield material, is yet another invalid name which cannot be validated by a diagnosis on present evidence; the Hopefield form is here regarded as *T. oswaldi* subsp. cf. *leakeyi*.

Palaeotaxonomy faces a number of difficulties not encountered in the classification of living groups (Simpson, 1943). The most obvious of these is incompleteness of data; forms can be distinguished only on the basis of bones and teeth, while soft-part anatomy, pelage details and even repertoires of social behaviour, all of which are often of taxonomic relevance in Primates, must remain unknown. In the Anthropoidea in particular, the pelage tends to be variable and of taxonomic value at the specific and subspecific level (presumably because of the dominance of vision and hence of visual cues in species-recognition by the animals themselves). In the majority of cases, as with *Simopithecus*, not even the skeletal and dental record is complete, so that features of key importance are often unrepresented in a sample of material. In addition, fossil sites are disparate in space and time, so that phenomena like geographical clines, important in living species, are rarely demonstrable.

In view of these difficulties, the most that can be claimed for the classification of subgenus *Simopithecus* presented here is that it is consistent with the evidence at present available, and has certain advantages over previous schemes. Species are separated by morphological differences, especially by different patterns of growth and proportions of skull and dentition, while differences in size and size-correlated characters are considered to indicate no more than subspecific separation. Populations which are not widely separate in time, and which on the basis of the incomplete record might have been given either subspecific or full specific status have been given the lower rank. This arrangement is consistent with the natural history of *Theropithecus* as an open-country form which is unlikely to have speciated excessively as a result of geographical isolation, and corresponds to the situation in, for instance, extant *Papio*.

This scheme also seems more reasonable on *a priori* grounds than previous conceptions which united *Simopithecus* material from Olduvai I to IV, with a time-span exceeding a million years, into a single subspecies, yet separated Olduvai IV material from specimens from contemporary sites only a few hundred miles away. The present scheme agrees fairly closely with other faunal evidence connecting sites in East and South Africa, especially Swartkrans with lower Olduvai II, Hopefield with late Olduvai IV. It is also more consistent, of course, with the 'long' timescale at Olduvai.

B. Relationships of the Genus

It remains to investigate the relationships of *Theropithecus*, as here expanded, within the Cercopithecoidea. Le Gros Clark (1964) and Simpson (1963) have emphasized the importance of distinguishing adaptive trends rather than static 'characters' when assessing the relationships of organisms. In Cercopithecoidea it is important also to recognize the effect of allometric and ontogenetic trends. Neither of the latter has always been sufficiently appreciated in previous descriptions of *Theropithecus*.

The following developmental and evolutionary trends are characteristic of *Theropithecus* as a whole:

The crowns of the cheek-teeth become more complex: especially in larger forms. This evolutionary trend was well under way by the first appearance of the genus at Makapan and Lothagam 3, but continued throughout its development, at least in the *Simopithecus* lineage.

The molars and premolars become more high-crowned and relatively larger.

The incisors are absolutely small in all forms, and relatively smaller in the larger ones. This feature, and the contrast with *Papio*, is shown in Fig. 23, where the transverse breadth between the lateral faces of the alveolae of the lower, lateral incisors is plotted against the combined length of the first two lower molars.

The male canines are relatively smaller, and the 'sectorial' face of P_3 shorter, in the larger-sized forms at each evolutionary stage. This effect becomes intensified in the course of evolution. Allomorphic trends in the dentition are thus directly opposite to those seen in *Papio*, in which the largest forms have relatively as well as absolutely the largest canines, incisors and P_3.

The mandibular ramus becomes relatively higher. This trend can only be traced from Kanjera/Olorgesailie to Olduvai IV, if indeed this is a time-series. Both allomorphosis and evolutionary development are probably involved, but the material is not sufficient to assess the importance of each. In either case, the trend is opposite

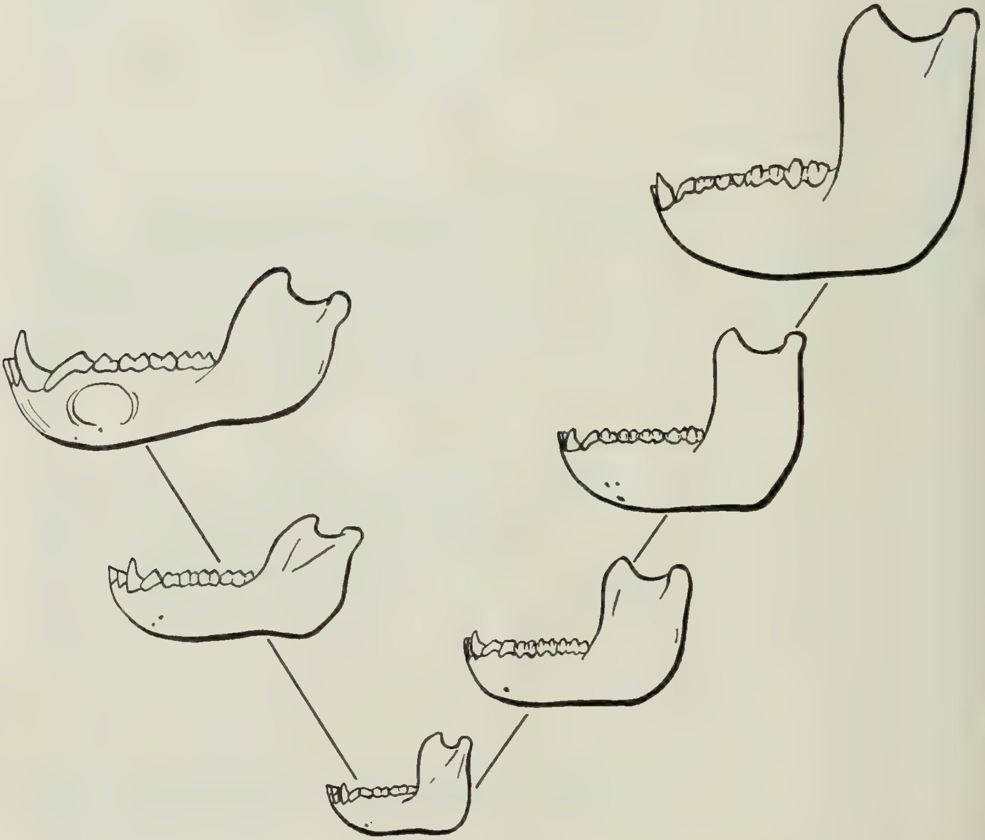


FIG. 22. Mandibular profiles of *Theropithecus* and *Papio*. Bottom: *Cercocebus torquatus* female (primitive shape in Papionini). Left line, ascending: *P. anubis*, female; *P. anubis*, male. Right line, ascending: *Theropithecus gelada*, female; *T. o. oswaldi*, female; *T. o. leakeyi*, female. Note contrasting allometric trends in two morphological series.

to that seen in other Cercopithecinae such as *Papio* in which the largest forms have the lowest rami, both absolutely and relative to corpus-length.

From the height of the ramus we can deduce that larger *Theropithecus* (especially at Olduvai IV) had a relatively larger glabella-prosthion dimension. This is also a feature of differential growth in *Papio* (Freedman, 1962b), and seems to be general in Cercopithecoidea (Jolly, 1965). In *Papio*, however, it is associated with an elongation of the basion-gnathion dimension, especially that part of it that is comprised of the tooth-row. In large *Theropithecus* the tooth-row is scarcely lengthened, but the posterior maxilla (and hence the mandibular ramus) is considerably deepened

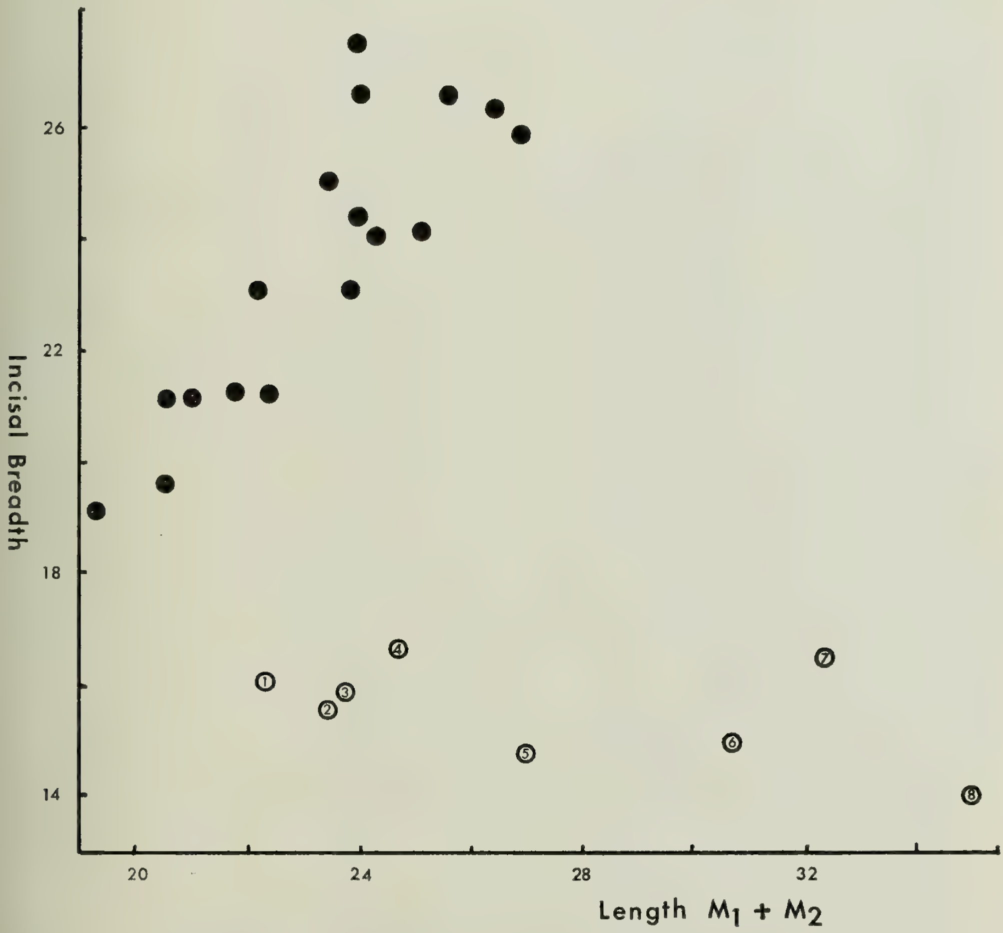


FIG. 23. Lower Incisal breadth plotted against combined length of M_1 and M_2. Open circles: *Theropithecus*. 1–3. *T. gelada* (males, AMNH). 4. Kanjera, ad. female (M. 11539). 5. Kanjera, juv. female (F 3398). 6. Olduvai IV, ad. female (*jonathani* type). 7. Olduvai II, juv. female (BK II). 8. Olorgesailie, ad. male (e). Solid circles: *Papio sp.* males and females, adults and juveniles, AMNH.

(Fig. 22). This difference in the shape of the maxilla may be partly due to the fact that the posterior molars are much larger, and apparently tended to erupt later, relative to the anterior dentition, in the large forms of *Theropithecus*. Thus, growth in the posterior maxilla might be expected to be prolonged, while that of the anterior part of the face was curtailed, when compared to forms such as *Papio*. Such a deepening would necessarily be accommodated by lengthening the vertical ascending ramus of the mandible. However, as described below, this feature may also be explained in functional and mechanical terms as a masticatory adaptation.

The temporal muscle originates relatively far forward on the braincase. Leakey and Whitworth (1958) quote the position of the meeting of the superior temporal lines ('at or about bregma in females, in front of bregma in males') as a character of *Simopithecus* distinguishing it from *Papio* in which they meet 'behind bregma'. This was questioned by Singer (1962), who rightly emphasised the variability of this character in *Papio*. There is, in fact, a valid distinction between *Theropithecus* on the one hand, and *Papio* and *Mandrillus* on the other, but it is less ambiguously defined in terms of ontogenetic process (Fig. 24). In all young Anthropoidea the temporal muscles are confined to the temporal fossa, from which they spread across the cranial vault as the jaws and dentition develop (Ashton and Zuckerman, 1956, Robinson, 1958). If growth continues after they meet in the midline, a sagittal ridge, then a crest, forms. Since the temporal muscles are known to grow even after sexual and dental maturity in *Papio* males, at least, (DeVore and Washburn, 1963), not even adults of like sex will necessarily show a similar pattern of lines and crests. *Theropithecus*, however, differs consistently from *Papio* and *Mandrillus* in the direction of temporal growth. The fibres spread fanwise from the temporal fossa, meeting first well forward on the cranial vault. The line of contact then lengthens back towards the inion and forwards to or beyond the bregma. This is the state reached in adult, Kanjera females. If further growth occurs (as in Kanjera males) a sagittal crest is formed along the line of contact. The crest itself is more or less even in height along its length, indicating uniform distribution of the temporal fibres. In *Papio*, growth in all but the earliest stages appears to be concentrated in the more posterior part of the temporal muscles. The temporal lines first meet at or very close to the inion. The line of junction moves only gradually towards the bregma as a sagittal crest forms adjacent to the inion. In *Mandrillus* the same growth-pattern is seen in a more exaggerated form. Here the posterior fibres of the Mm. temporales frequently meet at the inion early in their growth, but the sagittal crest, though it may become high and prominent, never advances more than two centimetres or so from the inion. The temporal lines in the region of the temporal fossa, and posteriorly well beyond the bregma, scarcely advance towards one another during growth, but frequently expand laterally to form, in adult males, broad flanges which roof the temporal fossae.

The forward position of the temporal muscles is certainly related to the vertical orientation of the mandibular ramus in *Theropithecus* and can also be related to the narrow postorbital region.

The short cranial base, with the transverse orientation of the auditory meatus seen in Kanjera *Simopithecus* may perhaps also belong to the same complex of features. If so, then the rather more oblique meatus of the Swartkrans and Olduvai II skulls might indicate that the trends towards vertical rami and forwardly located temporal muscles had advanced less far in these earlier forms. The evidence is tenuous, however, and needs to be supported by more complete skulls and mandibles from the sites concerned.

Although the height of its cheek-tooth crowns and orientation of the temporal musculature superficially recall the leaf-monkeys, there is no doubt that these

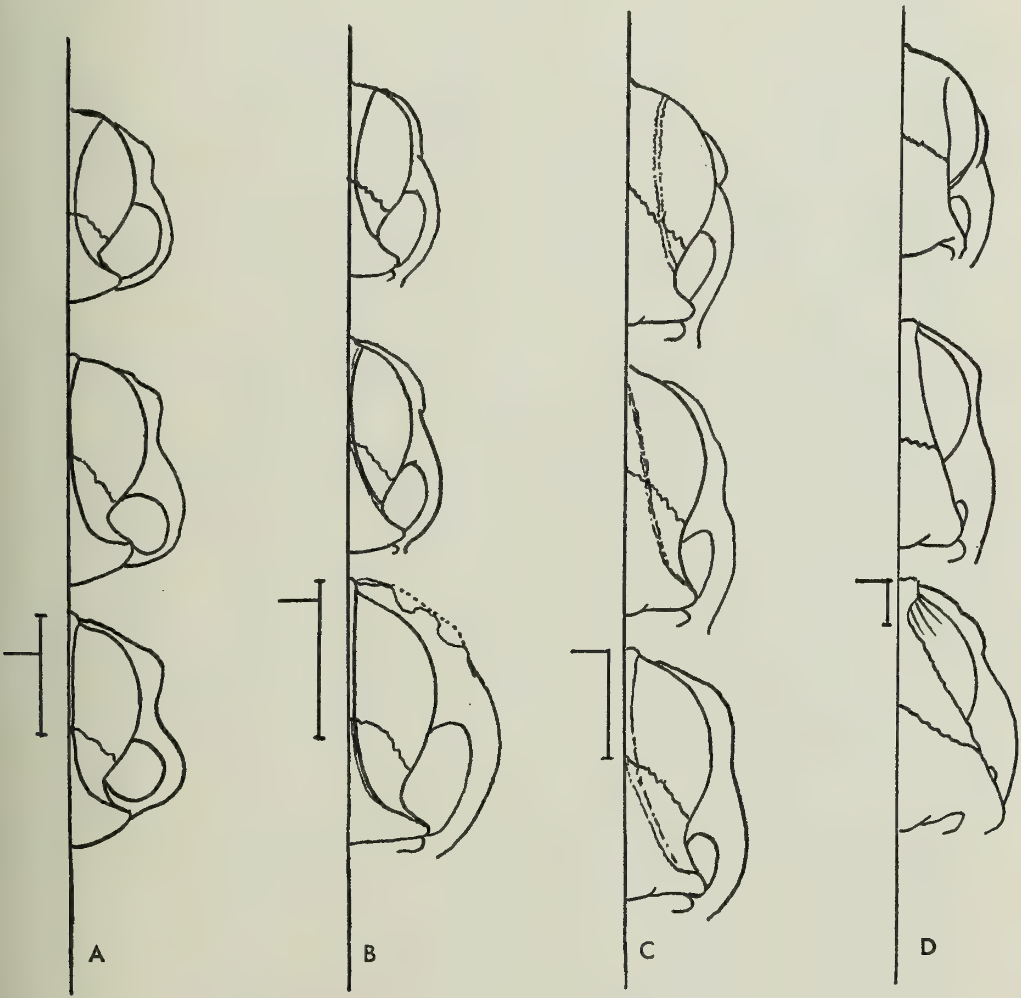


FIG. 24. Series of half-calvaria, from above, to show development of temporal lines and crests in large Papionini. A. *T. gelada*. Top to bottom: adult female, young adult male, old male. B. *T. o. oswaldi*. Sub-adult female, adult female, young adult male. C. *P. anubis*. Sub-adult male, adult male, adult male with exceptional crest. D. *Mandrillus leucophaeus*. Sub-adult male, adult male, old male.

resemblances are due to adaptive convergence, and that *Theropithecus* is, as has been universally recognized, allied with other Cercopithecoidea which have cheek-pouches but lack sacculated stomachs (Cercopithecinae of Simpson, 1945, Kuhn, 1967, Jolly, 1966, and most other authors; Cercopithecidae of Hill, 1966, following Pocock, 1925). Within this group, Garrod (1879), arguing from the structure of the liver, allied the genus with *Cercopithecus* rather than *Papio*, which would put it in the tribe Cercopithecini of Jolly (1966) and Kuhn (1967) (the subfamily Cercopithecinae of Hill, 1966). With this one dubious exception, the structure of *Theropithecus* from the molecular (Chiarelli, 1968, Sarich, 1971) to the behavioural (Crook, 1966) level, differs from that of the guenons and their allies, agreeing more closely with that of the remaining Cercopithecinae. Kuhn (1967) accordingly places the genus in his tribe Papionini (equivalent to Cynopithecinae of Hill, 1966) which includes all Cercopithecinae apart from the guenon group. Leakey (1965) presumably expresses a similar view by putting *Simopithecus* into the family Cercopithecidae, subfamily Cynocephalinae, which includes *Papio*, but is otherwise indeterminate. Jolly (1966) suggested that *Theropithecus* (and *Simopithecus*, which was regarded as generically distinct) should be put into a separate cercopithecine tribe, giving three co-ordinate groups: Cercopithecini, Cercocebini, and Theropithecini. It was recognized that the Theropithecini show many characteristics, such as a hypoconulid on M_3, chromosome number and details of the karyotype, indicating a common origin with the Cercocebini, but their many distinctive features were felt to merit more than generic separation. At the time, the natural history of the gelada was poorly reported and believed to be essentially similar to that of *Papio*; there was therefore no obvious functional explanation for its peculiarities, especially its extreme adaptation to terrestrial life, which could only be explained in terms of a long, separate evolutionary development. Recent studies by Crook (1966, 1967, 1968), however, have made it clear that most, if not all, the features that distinguish the gelada from other 42-chromosome monkeys are related functionally to its way of life, which is fundamentally different from anything seen in other living monkeys, not excluding *Papio* (see next section). If the peculiarities of *Theropithecus* are regarded as a single adaptive complex, they need not indicate a very remote separation of the lineage from other Cercopithecinae. It is therefore suggested that *Theropithecus* should be regarded as a rather distinct genus of the Cercocebini (= Papionini of Kuhn, 1967, which is the nomenclatorially correct *nomen*).

Hill (1968), in his rather more inflated classification of Cercopithecinae, retains Theropithecini as of Jolly (1966), but with the addition of *Libypithecus* Stromer, as a tribe *within* Cynopithecinae (= Papionini of Kuhn and this work) co-ordinate with tribes Cercocebini (macaques and mangabeys) and Papionini (*Papio*, *Mandrillus*, *Parapapio* and *Procynocephalus*). Without entering into discussion of the naturalness of the latter two tribes, which seems questionable, we might note that Hill's classification expresses a concept of the relative separateness of *Theropithecus* (*sensu lato*) from other 42-chromosome monkeys essentially similar to that suggested here.

At the other extreme, Buettner-Janusch (1966a, 1966b) has suggested that *Papio*, *Mandrillus*, *Theropithecus*, (and presumably *Cercocebus*) should be included in a single genus, *Papio*. This arrangement would imply the inclusion also of *Dinopithecus*, *Gorgopithecus*, *Parapapio* and *Procynocephalus* to produce a grouping coincident with tribe Papionini, as here accepted. Some of these fossil genera may well prove undefinable. Most are, however, better based than, for instance the many genera of mid-Tertiary Hominoidea which have recently been combined (Simons and Pilbeam, 1965). To lump them uncritically is to obscure the undoubted fact that the large, non-rainforest Cercopithecoidea, especially in Africa, showed much more diversity, and, by implication, much more ecological specialization, in the Plio-Pleistocene than is the case today. Part of the difficulty arises from the fact that the Cercopithecinae, like the Bovidae, are a group which has undergone extensive speciation and radiation comparatively recently. The problem lies in expressing this diversity in a useful and phyletically accurate way while not inflating the classification of the group to the point where it obscures the considerable similarity at the genetic level, which is manifested in their 'crossability' under artificial conditions, (Chiarelli, 1968). In the scheme adopted here a balance is struck by, on the the one hand, making genera of monophyletic groups of species sharing a common major adaptive trend (Simpson, 1963), while on the other, expressing the close genetic relationship between genera by grouping them in a single low level taxon, a tribe.

The interrelationships among the closely related genera within Papionini are not easy to deduce, much of the evidence being contradictory. Dental, cranial, genital and behavioural characteristics, for instance, suggest that *Papio*, *Mandrillus* and *Cercocebus* are more closely related to each other than to the rest, but chromosomal structure (Chiarelli, 1968) indicates that *Cercocebus* is distinct from the others. The describer of *T. gelada* (Rüppell, 1835) put it in the genus *Macacus* (i.e. *Macaca*). Certain behavioural traits (T. E. Rowell, pers. comm.) and the dispersed nature of the female 'sexual skin' (Matthews, 1956) recall macaques rather than living African Papionini. The unhollowed maxilla of late *Simopithecus* is also macaque-like, but is not primitive to the genus. Various authors, of whom Buettner-Janusch (1966) is the most recent, have allied *T. gelada* (and by implication fossil forms of the genus) with *Papio* (*sensu stricto*). Chromosomal structure (Chiarelli, 1968) is in accord with this view but anatomical evidence is not; their resemblances are superficial and easily accounted for by modest convergence, while those characteristics of *Papio* which are not related to its absolute size or terrestrial adaptation again ally it more closely with mangabeys and mandrills. Jolly (1966) suggested that *Dinopithecus* and *Gorgopithecus* might be placed in the Theropithecini because of resemblances to *Simopithecus* (= *Theropithecus*) in molar structure noted by Freedman (1957). Both are known only from South African sites, and have been described by Freedman (1957). Casts of some of the South African material were examined.

Dinopithecus is known from Swartkrans and Schurweberg, perhaps also Sterkfontein and Kromdraai. Its facial and cranial shape, length of muzzle and orientation of the mandibular ramus are such as might be expected in contemporary populations of the *Theropithecus* line, but its dental structure does not show the characteristic *Theropithecus* characters, and this separates it from *Theropithecus darti danieli* which is also found at Swartkrans (Freedman, 1957).

Gorgopithecus is found only at Kromdraai (Freedman, 1957), believed to be the latest and 'wettest' of the Transvaal australopithecine caves (Brain, 1958). Its molars are very like those of *Dinopithecus* but it has a shorter, deeply-hollowed maxilla, and, unlike most other Cercopithecoidea, including *Dinopithecus*, apparently lacks sexual dimorphism in general size, although the usual sex-differences in canines and P_3 are present. It shows no tendency to evolve in the direction of *Theropithecus*. *Dinopithecus* and *Gorgopithecus* thus seem to represent another line of Papionini, perhaps close in origin to *Theropithecus*, but evolving in a different direction. As far as is known, it left no descendants after the earliest Middle Pleistocene.

Perhaps the most reasonable view is that *Theropithecus* is an offshoot of an African papionine stock, which had already sent colonists (the ancestors of the macaques) to Eurasia, and which was later to give rise to *Papio*, *Mandrillus* and *Cercocebus*. The macaque-like characteristics of *Theropithecus* would thus be primitive, while those it shares with the African Papionini are due to a period of common ancestry.

The time of differentiation of the genus will undoubtedly be more clearly defined when more Cercopithecidae are described from the Pliocene of Kenya (Bishop and Chapman, 1970; Patterson, Behrensmeyer and Sill, 1970). At the present, the upper limit is set at about four million years by the occurence of a single *Theropithecus* molar at Lothagam 3 (Patterson, Behrensmeyer and Sill, 1970).

A taxonomic summary of *Theropithecus* follows:

Family: **CERCOPITHECIDAE** Gray 1821
Subfamily: **CERCOPITHECINAE**
Tribe: **PAPIONINI** Burnett 1828

Genus ***THEROPITHECUS*** Geoffroy 1843
GELADA Gray 1843; ***SIMOPITHECUS*** Andrews 1916;
BRACHYGNATHOPITHECUS Kitching 1952, in part

TYPE-SPECIES. *Theropithecus gelada* (Rüppell) 1835.

DIAGNOSIS: Differs from other Papionini by progressive development of the follwing characters: incisors small, and relatively *smaller* in larger forms; ascending ramus of mandible vertical, even in largest forms; ascending ramus of mandible *higher* in larger forms; molars and premolars large, broad, with high and complex crowns; postcranial skeleton highly adapted for terrestrial life; index finger very short. (Soft-part characters, known only in *T. gelada*, but probably part of the adaptive complex of the genus: sexual skin of females pectoral; accessory sitting-pads present; ischial callosities not confluent in males.)

DISTRIBUTION. Africa, mid-Pliocene to Recent.

Sub-genus: ***THEROPITHECUS*** (new rank)
Genus ***THEROPITHECUS*** auct.

TYPE-SPECIES. *T. gelada* (Rüppell) 1835.

DIAGNOSIS. A lineage of *Theropithecus* in which a somewhat primitive molar structure is retained, male canine and P_3 are scarcely reduced relative to the molars, deep mandibular and maxillary fossae are invariably present, especially in males, and the mandible deepens appreciably towards the symphysis. The superior surface of the symphysis is excavated. Specialisations of the sub-genus include: a high, convex premaxilla, narrow nasal aperture, and pre-nasal tubercles.

DISTRIBUTION: High plateau of central Ethiopia; Recent.

Theropithecus (Theropithecus) gelada (Rüppell 1835)

Macacus gelada Rüppell 1835; *Gelada rueppelli* Gray 1843; *Papio gelada* auct.

DIAGNOSIS AND DISTRIBUTION: As subgenus.

Subgenus ***SIMOPITHECUS***, new rank

Genus ***SIMOPITHECUS*** Andrews 1916, and most later authors

TYPE SPECIES. *Simopithecus oswaldi* Andrews 1916.

DIAGNOSIS: Lineage of *Theropithecus* distinguished from the typical subgenus by the following evolutionary trends: retention of primitive shape of premaxilla and nasal aperture; progressive loss of mandibular and maxillary fossae, reduction of male canine-P_3 complex; symphysis becoming shallower and less excavated superiorly, inferior border of corpus becoming more nearly parallel to occlusal plane; molars and premolars becoming even more complex. Body-build more robust. Tendency towards delayed eruption of third molars.

Theropithecus (Simopithecus) oswaldi (Andrews 1916)

Simopithecus oswaldi Andrews 1916; *Simopithecus leakeyi* Hopwood 1934 (in part); *Simopithecus jonathani* Leakey and Whitworth 1958.

HOLOTYPE. Female mandible, M 11537, from Kanjera; housed in the Department of Palaeontology, British Museum (Natural History), London.

DIAGNOSIS. More advanced than *T. darti*; maxillary and mandibular fossae are always absent or very weak, female muzzle lower anteriorly, male mandible not deepening anteriorly, superior surface of symphysis almost flat, male canine and P_3 relatively reduced, especially in larger forms.

DISTRIBUTION. Africa, from Cape of Good Hope to Algerian coast, Middle to Upper Pleistocene.

Subspecies: ***T. (Simopithecus) oswaldi oswaldi*** (Andrews 1916)

Simopithecus oswaldi Andrews 1916; *S. oswaldi oswaldi* Leakey and Whitworth 1958.

HOLOTYPE. As species.

HYPODIGM. Kanjera series, as listed above.

DIAGNOSIS. Small and somewhat less specialized than other known subspecies.

DISTRIBUTION. Kanjera.

T. (Simopithecus) oswaldi leakeyi (Hopwood 1934)

Simopithecus leakeyi Hopwood 1934 (in part); *S. oswaldi olduvaiensis* Leakey & Whitworth 1958; *S. jonathani* Leakey & Whitworth 1958; *S. oswaldi leakeyi* Leakey 1965

HOLOTYPE. Male mandibular fragment, M 14680, from Olduvai Bed IV, housed in the Department of Palaeontology, British Museum (Natural History), London.

HYPODIGM. Olduvai IV series as listed above.

DIAGNOSIS. Cheek-teeth much larger than in typical sub-species, somewhat larger than in *T. oswaldi mariae.* Male lower third premolar even more extremely reduced than in *T. oswaldi mariae.*

DISTRIBUTION. Olduvai IV, ? Hopefield (cf.)

T. (Simopithecus) oswaldi mariae subsp. nov.

Simopithecus oswaldi mariae Leakey & Whitworth 1958 (nom. nud.)

HOLOTYPE. An adult female mandibular corpus KNM–OG 0002, with complete cheek-tooth row, from Olorgesailie, labelled 'Site 10, Bed B, Tr. Fr.'; 'f' in descriptive list, p. 45. Housed in the Kenya National Museum, Nairobi.

HYPODIGM. Olorgesailie series, as listed above.

DIAGNOSIS. Body size and molar size larger than nominate subspecies, but smaller than *T. oswaldi leakeyi.* Male canine lower-crowned, P_3 shorter and broader than in *T. o. oswaldi,* but less extreme than in *leakeyi.*

DISTRIBUTION. Olorgesailie; ? Ternifine (cf.)

Theropithecus (Simopithecus) darti (Broom & Jensen 1946)

Simopithecus leakeyi Hopwood 1934 (in part); *Papio darti* Broom & Jensen 1946; *Brachygnathopithecus peppercorni* Kitching 1952; *Gorgopithecus wellsi* Kitching 1953; *Gorgopithecus darti* Kitching 1953; *Simopithecus darti* Freedman 1957; *Simopithecus danieli* Freedman 1957; *Simopithecus oswaldi* Leakey & Whitworth 1958 (in part)

HOLOTYPE. A damaged male mandible, M 201, 1326/1, housed at the University of the Witwatersrand, Johannesburg. (Freedman 1957).

DIAGNOSIS. A successional species ancestral to *T. oswaldi,* retaining primitive gnathic and dental characteristics, especially a longer male P_3 and high-crowned male canine. Female anterior muzzle probably also higher than in *T. oswaldi.*

DISTRIBUTION: ? late Pliocene to early Pleistocene, East and South Africa.

Subspecies: ***T. (Simopithecus) darti darti*** (Broom & Jensen 1946)

Papio darti Broom and Jensen 1946; *Simopithecus darti* Freedman 1957: *S. oswaldi darti* Singer 1962

HOLOTYPE. As species.

HYPODIGM. Makapan series ascribed to *Simopithecus darti* by Freedman (1957, 1960.)

DIAGNOSIS. Smaller than other subspecies, with characteristics recalling subgenus *Theropithecus*; primitive molar structure, high crowned male canines and long P_3, gelada-like symphysial profile and at least occasionally a deep mandibular fossa.

DISTRIBUTION. Makapan.

T. (Simopithecus) darti danieli (Freedman 1957)

Simopithecus danieli Freedman 1957; *S. oswaldi danieli* Singer 1962

HOLOTYPE. A female muzzle and two halves of the mandible from Swartkrans, SK 563/402/405, housed in the Transvaal Museum (Freedman 1957).

HYPODIGM. Swartkrans series ascribed to *S. danieli* by Freedman (1957).

DIAGNOSIS. Larger than nominate subspecies; dental and gnathic structure less primitive, tending towards *T. oswaldi*.

DISTRIBUTION. Swartkrans, Olduvai I and/or lower II (cf.)

VI. THE NATURAL HISTORY OF *SIMOPITHECUS*

The natural history of a fossil animal can never be completely reconstructed, but some conclusions about it can often be drawn from evidence of two main kinds. First, it is often possible, from a study of the context in which the animal is found as a fossil, to deduce in broad terms the climatico-vegetational zone in which it lived, and perhaps also to guess that particular surroundings within that zone were its preferred habitat. The context itself is divisible into two categories, the biotic and the geological. The first, the accompanying fossil flora and fauna, must be treated with caution since animals and plants from a variety of zones are not infrequently gathered in artificial association after death. The second, the geological context, is rarely unambiguous in its climatic implications (witness the 'pluvial' controversy).

The second major category of information is derived from the structure of the fossil animal itself, by recognition and interpretation of the adaptations of the form to its environment. It is important to distinguish between genetically-determined adaptations – fixed in the species by the action of natural selection – and the phenotypic adaptations made by the individual animal in the course of its lifetime of interaction with the environment. The distinction is important because inherited adaptations can persist in an ecological situation other than that in which they were evolved (the 'brachiator' characters of the mountain gorilla are a case in point), and hence give a false impression of the current way of life of the animal concerned. On the other hand, the existence of a genetically-determined adaptation in a species attest to a long period of selection under particular conditions, and hence are good evidence for or against long-term occupation of a particular ecological niche. In structures like bones which are relatively plastic to environmental influence even in the mature animal, it is often difficult to distinguish the effects of the two components of adaptation. In dentition the distinction should be easier; the major features of tooth size and cusp disposition may be assumed to be genetically-determined, while environmental effects are obvious in patterns of wear and perhaps such features as hypoplastic enamel bands. Interpretation of the anatomical evidence for the ecology of a fossil form rests very largely upon analogies drawn with living animals whose way of life is known.

The natural history of the Cercopithecinae varies widely among species. The range of the group as a whole includes all tropical vegetational types from rainforest to semi-desert *sahel*, and also various subtropical, warm-temperate and montane forests and woodlands. Within each broad habitat, different species show preferences for different kinds of country, and even forms that are sympatric are usually found on close study to exploit rather different aspects of their environment (Booth 1956, Hall, 1965). Some tropical rain-forest Cercopithecinae, and most of those inhabiting other vegetational zones, forage on the ground as well as in trees and are more or less adapted to terrestrial quadrupedalism. In a few species, most or all of the foraging time is spent on the ground; these have been distinguished as 'baboons' (Jolly, 1967).

Of particular relevance to reconstructing the natural history of Pleistocene *Theropithecus* is the ecology of the sole living representative of the genus, *T. gelada*, especially when this is compared with that of baboons of other genera, such as *Erythrocebus** and *Papio*. Early reports of the natural history of *Theropithecus* (Rüppell, 1835; Starck and Frick, 1958) have recently been supplemented by more detailed ecological data derived from prolonged field work (Crook, 1966, 1967, Crook and Aldrich-Blake, 1968).

The gelada is confined to the high plateau of Ethiopia, where it lives above the treeline. It is commonly associated with steep rock-faces and gorges, upon which it sleeps and takes refuge if attacked. Herds numbering up to 300 animals forage on the open, short-grass country, dissected by the gorges, where trees do not occur. Foods listed by Crook include a high proportion of rhizomes, blades and seeds of grasses together with stems and bulbs of other herbaceous plants. Fruits, bark, leaves and other tree products are rarely available and are scarcely exploited when they are. Like other Cercopithecinae, geladas eat small vertebrate and invertebrate animals when they come across them (P. Lisowski, pers. comm.) The gelada has a unique and characteristic way of feeding. Most of its time is spent in a sitting position, picking up small objects by hand using a precise, thumb-index grip, while shuffling slowly forward on its haunches. Frequently, areas of turf are torn up using both hands, to expose the roots. Crook plausibly suggests that the pectoral, rather than perineal, position of the female sexual skin is adaptive to this feeding position. The pair of fat-filled cushions situated ventral to the ischial callosities (Pocock, 1925) may be seen as further adaptation to habitual sitting on the ground while feeding.

Modern *Papio*-baboons are extremely widespread in trans-Saharan Africa, and inhabit all vegetational zones from semi-desert scrub to tropical rain-forest. Throughout their range they are opportunist and eclectic feeders. Forest-dwelling baboons of the Eastern Congo and parts of Uganda feed to a large extent upon the fruit of trees such as figs and *Maesopsis*. Those living under savannah conditions have been observed to climb *Acacia* trees to gather fruits and ant-galls. The feeding-methods of *Papio* are variable. When feeding upon small, concentrated objects such as grass-blades, it may sit, gelada-fashion, and pick them up, using both hands. A more characteristic feeding pattern, however, associated with larger but more scattered food-objects, is to stand 'tripedally', conveying food to the mouth with the free hand (Crook and Aldrich-Blake, 1968). On the ground, a wide variety of herbs is eaten, including blades and rhizomes of grass, tubers, seeds and fruits; parts of grasses make up the bulk of the diet of groups living in relatively treeless areas like parts of the Nairobi National Park (DeVore and Washburn, 1963). Animal food, consisting mainly of invertebrates and small vertebrates such as lizards, is regularly taken. Over the greater part of its range *Papio* is currently the only ground-living monkey, allowing it to exploit the full range of food-resources in its habitat. In much of the Sudanic belt and parts of East Africa, however, it shares its habitat with *Erythrocebus*, and the two forms exploit rather different aspects of the environment. The patas monkey is able to move independently of large trees and permanent water, and rarely enters the belt of trees that occurs along water-courses. *Papio* is typically to be found in the riverain strip in which it sleeps and from which it forages out into open country by day (Hall, 1965). More significant for the reconstruction of the Pleistocene ecology of the genus is its behaviour (described by Crook and Aldrich-Blake, 1968) in the small area of Ethiopia in which *Theropithecus* occurs. Here *Papio* is confined to woodland, and its diet includes a high proportion of tree-products. It does not occur in the open, treeless grassland inhabited by *Theropithecus*. Comparisons between *Theropithecus* (ancient and modern) and *Papio* in postcranial, cranial and dental anatomy are entirely consistent with the hypothesis that the same ecological distinction between the two genera existed during the Pleistocene, when both were equally widespread, and is the basis of the many adaptational trends which distinguish them.

**Erythrocebus*, the patas monkey, is related phyletically to *Cercopithecus*, but is a baboon by the behavioural criterion (Jolly, 1967).

A. HABITAT

The geological evidence of the climate of Olduvai in the Early and Middle Pleistocene is somewhat ambiguous. Hay (1963) emphasizes that minerals deposited among the lake sediments are indicators of dry climate with high evaporation rates throughout most of the history of the lake, producing saline and alkaline conditions in its waters. Leakey (1951, 1965) maintains that a *lower* evaporation/precipitation ratio than that existing in the region today would be necessary to account for the persistence of a lake throughout much of the Pleistocene, and points to the occurrence of frequent fish, crocodile and hippopotamus remains as evidence for the freshness of its waters. A likely explanation seems to be that while the main body of the lake waters may have been saline, fresh water occurred around the lake margins near the mouths of feeder-streams, and may have overlain the heavier saline waters over most of the lake surface. It would seem too that Lake Olduvai fluctuated widely in extent and salinity during its history, due to the complex interaction of variable evaporation, precipitation, catchment and drainage, the latter two factors being liable to alteration by tectonic movements.

Cooke's (1963) conclusion, that the Olduvai area was within the broad vegetational category between desert and rain-forest throughout its known history seems reasonable on faunal and climatic evidence. Variations in local climate probably produced vegetational fluctuations at most between semi-desert and moist, wooded savannah. The immediate faunal context has been reported for only one of the Olduvai *Theropithecus* sites – BK II, and is said by Leakey (1963) to imply 'lush vegetation'.

The Bed IV *Theropithecus* also lived, or at least was preserved as a fossil, in a waterside habitat, consisting of a flood-plain channelled by streams (Hay, 1963).

The geological and faunal context of *T. oswaldi* at Kanjera is essentially similar, with a lakeside setting and savannah fauna (Kent, 1942), and so is Kaiso.

The Plio-Pleistocene Omo beds were apparently laid down by the large, primaeval Omo River, and in the bed of the lake which it fed (Butzer and Thurber, 1969). Permanent, fresh water was undoubtedly present. The habitat is believed to have been not unlike that of the present day, with dense bush and gallery forest in the immediate vicinity of the river banks, giving way rather abruptly to drier and more open savannah-woodland (F. C. Howell, pers. comm.)

Isaac (1966b) describes the Olorgesailie basin at the time of its occupation by *Theropithecus* and Acheulian man. 'The fresh-water, mostly shallow, lake was normally surrounded by swamps and alluvial flats, which, from the evidence of root-channelling in the sediments appear to have been heavily vegetated with grasses and perhaps shrubs.' (p. 135) '. . . the seasonal stream-channels would have been the only bald patches in vast areas of thick grass and shrubs.' (p. 142). A higher rainfall, or at least a lower evaporation/precipitation ratio' must be postulated to account for the persistence of permanent fresh water in a basin which today supports only an intermittent swamp (Isaac, 1966a).

The climatic conditions existing at the time of the filling of the Transvaal caves have been reconstructed by Brain (1958), using petrological analysis. The Makapan fossiliferous breccia probably accumulated under conditions of 'some aridity', with a rainfall less than that of the present day, which is sufficient to support a 'bushveld' (Cooke, 1963). The Swartkrans breccia was apparently formed under conditions not far removed from those of the present, with 'temperate mixed grassland' the vegetational type (Cooke, 1963), though there is evidence for a minor dry oscillation within the deposit.

The sandy rock containing the Hopefield material is believed to represent the indurated remains of coastal dunes, among which lay vleis, shallow freshwater lagoons (Singer, 1962; Singer and Keen, 1955; Keen and Singer, 1956).

Pleistocene *Theropithecus* was clearly not confined to any one major climatic zone, ranging in latitude from the Equator to the Cape of Good Hope and the Algerian coast. Nor is it associated with any major vegetational zone, beyond the fact that none of its occurrences are among a tropical rain-forest fauna, an observation of dubious value since no such sites are known from this time period. It is striking, however, that wherever it is found, Pleistocene *Theropithecus* is associated with geological and faunal evidence for standing fresh water, usually shallow lakes surrounded by extensive alluvial flats and fed by sluggish rivers. By itself, this observation would be of little significance in reconstructing the ecological relationships of *Theropithecus* in the Pleistocene, since such depositional conditions are obviously ideal for fossilisation, as well as conducive to the accumulation of bones in ecologically meaningless death-assemblages. It assumes greater significance, however, if combined with the negative evidence of other sites at which *Theropithecus* is rare or absent. Table 13 is a list of the more important Plio-Pleistocene faunal sites in East and South Africa from which monkeys are reported. Group I are, from geological evidence, riverain, lake, or swamp deposits. All have hippopotamus, a good faunal indicator of fresh water. Group II sites are mostly caves, with no geological evidence for surface water nearby. Laetolil alone is subaerial. Hippopotamus is absent from Group II sites, apart from Makapan.

Table 13 also indicates the status of *Theropithecus* at each of the sites. It is either the only monkey, or the most frequent one, at all but one of the Group I sites. (The exception, Kanam, has yielded no baboon material at all, but only the remains of a single colobine monkey, as yet undescribed). It is completely absent from Laetolil and six of the eight cave sites. In the remaining two cave sites it is present, but outnumbered by other baboons, especially *Papio* and *Parapapio*. It may be significant that one of these two caves (Makapan) is the only one from which *Hippopotamus* has been reported, while of the three caves from which there are records of swamp-dwelling rodents, *Pelomys* or *Dasymys*, two are Makapan and Swartkrans.

TABLE 13

Indications of the habitat of fossil *Theropithecus*

	Thero-pithecus	*Papio/ Parapapio*	*Cerco-pithecoides*	*Gorgo-pithecus*	*Dino-pithecus*	*Hippo-potamus* sp.	*'Waterside' Rodents*
I 'Waterside' sites:							
Hopefield	A	—	—	—	—	X	
Olduvai I and basal II	A	—	—	—	—	X	
Olduvai Upper II	A	B	—	—	—	X	
Olduvai Upper IV	A	B	—	—	—	X	
Kaiso	A	—	—	—	—	X	
Kanam	—	—	—	—	—	X	
Omo	A	—	—	—	—	X	
Kanjera	A	—	—	—	—	X	
Olorgesailie	A	—	—	—	—	X	
Koobi Fora	A	—	—	—	—	X	
II 'Dry' sites:							
Taung	—	A	X	—	—	—	
Makapan	B	A	X	—	—	X	X[1]
Sterkfontein	—	A	X	—	X	—	
Bolt's Farm	—	A	X	—	—	—	X[2]
Gladysvale	—	A	—	—	—	—	
Swartkrans	B	A	X	—	X	—	X[2]
Kromdraai	—	A	—	X	X	—	
Laetolil	—	A	—	—	—	X	

Statuses:

(*Theropithecus*, *Papio* and *Parapapio*):

A: Only, or most common monkey

B: Present, but less common than other form

Other monkeys, rodents and *Hippopotamus*:

X: Present

Data for monkeys from Freedman, 1957; other fauna from Cooke, 1963

[1] *Pelomys*

[2] *Dasymys*

From such evidence it seems reasonable to infer that *Theropithecus* populations living in the lowlands of tropical Africa during the Pleistocene frequented preferentially the alluvial flats surrounding shallow lakes and vleis. Such areas would, as indicated by Isaac (1966b) support a rich and dense ground-flora, especially grasses, but, being liable to season flooding, are unlikely to have been wooded or forested. There is thus a distinct parallel to the habitat-preference of *T. gelada*, which also avoids woodlands in favour of open grasslands.

B. ANATOMICAL INDICATIONS OF MOTOR HABITS

The available long-bones do not permit accurate limb-proportional indices to be calculated. Of the commonly used indices, the brachial index (Radius Length × 100/Humeral Length) and the humero-femoral index (Humerus Length × 100/ Femoral Length) can be estimated for *T. oswaldi oswaldi*, and the latter for *T. oswaldi mariae*. There are however, no recognizable associated sets from single individuals, all bones have to be sexed by guesswork, and unbroken lengths estimated (section II). Errors arising are likely to be large and are compounded when the estimates are used to calculate indices. The values obtained for the indices must therefore be regarded as crude approximations only. Nevertheless, when these estimated dimensions are plotted against those of other Cercopithecinae, (Figs 25, 26), the data from both sexes of both subspecies are consistent in suggesting that *Simopithecus* was at the extreme edge of the range of large Cercopithecinae in its high humero-femoral, and low brachial index.

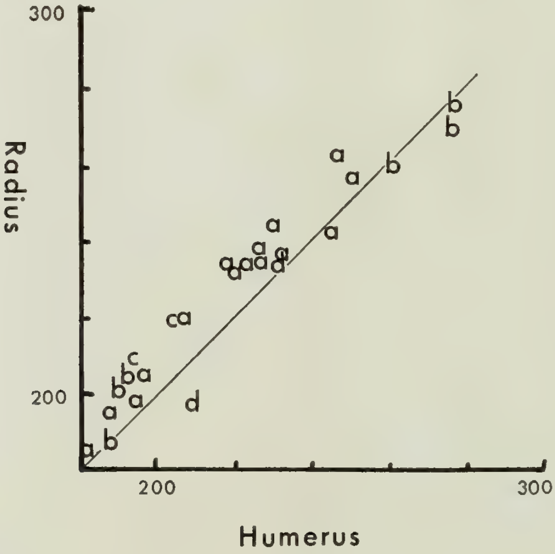


FIG. 25. Relationship between humeral and radial length in Papionini. a. *Papio*. b. *Mandrillus*. c. *T. gelada*. d. *T. owsaldi oswaldi*, male and female. Diagonal line represents humerus = radius in length.

TABLE 14

Limb-proportions in *Theropithecus*

The lengths of the segments in the fossil forms are estimated as described in the text

	Lengths (mm)			R/H	H/F	R/F
	Humerus	Radius	Femur			
Kanjera Large male	c 235	224	234	95·3	100·4	95·7
Kanjera Large female	209	198	201	94·7	104·0	98·5
Olorgesailie Male	c 290	—	297	—	c 97·6	—
Olorgesailie Female	c 240	—	232	—	c 103·4	—
T. gelada Male (U. Primatology)	194	210	209	108·2	92·8	100·5
T. gelada Male (AM 60568)	204	220	212	107·8	96·3	103·8

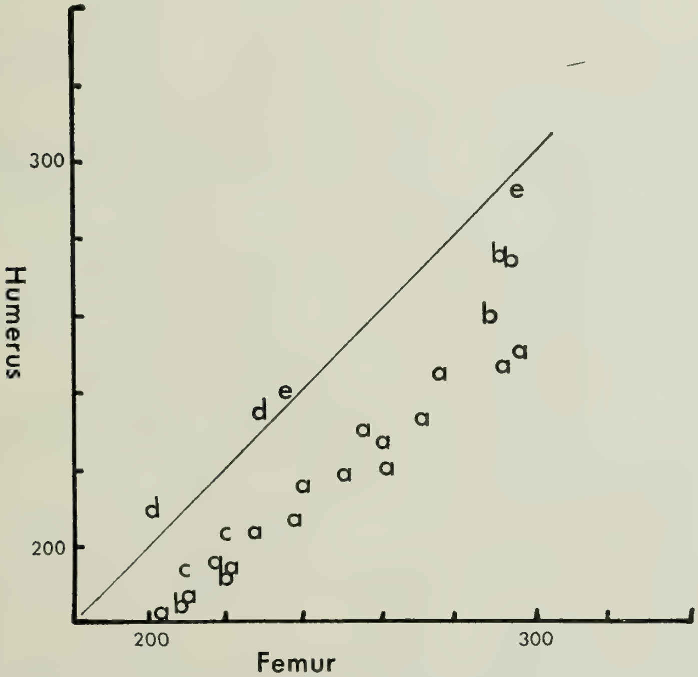


FIG. 26. Relationship between humeral and femoral length in Papionini. a. *Papio*. b. *Mandrillus*. c. *T. gelada*. d. *T. oswaldi oswaldi*, male and female. e. *T. oswaldi mariae*, male and female.

Among living Cercopithecinae, a tendency towards equality of femoral and humeral lengths is characteristic of terrestrial adaptation, especially among Papionini (Jolly, 1965). It is associated with an increase of the length of the upper arm, and of the arm as a whole, relative to the trunk length, as is presumably adaptive to locomotion predominantly upon level surfaces. The relatively long humerus of *Simopithecus* may be seen as a result of the trend carried to an extreme in a highly terrestrial form. However, it is also possible that its sedentary feeding habits were also a factor, especially since the robusticity of the femur indicates that the high index might be due to shortening of the thigh as much as to lengthening of the arm. In this connection, it may be significant that *Gorilla*, also a large, terrestrial, heavily-built, somewhat sedentary feeder, has the highest humero-femoral index among apes.

In its relatively short forearm. *Simopithecus* contrasts with *Theropithecus gelada*. In the extant Cercopithecinae, elongation of the fore-arm is associated with a terrestrial, cursorial gait, in both Papionini and Cercopithecini, presumably as an adaptation to fast running by lengthening the effective stride (Jolly, 1965, 1967). Among the Pongidae, the longest forearms are again associated with agility, but in this case it is acrobatic skills in climbing and brachiation that are involved, and the milieu is arboreal rather than terrestrial, the shortest forearm being found in the terrestrial but comparatively slow-moving gorilla. The short forearms of *Simopithecus* therefore do not conflict with the structural evidence for terrestrial habits, but simply reinforce the evidence of its robust skeleton that it was poorly adapted for rapid movement of any sort. In this it contrasts rather markedly with the living gelada.

It is possible to distinguish a number of features of the limb-bones of extant baboons which are correlated with adaptation to life on the ground. In most cases, it is also possible to suggest a plausible explanation of the characters in terms of advantage conferred in terrestrial locomotion (Jolly, 1964; 1967). Taken together, these characters form a single consistent functional pattern (Napier and Davis, 1959). Elements of this pattern are indicated by limb-bones of *Simopithecus* from each of the sites at which the post-cranial skeleton is represented.

The short, anteriorly curved femur of *Theropithecus oswaldi oswaldi* at once precludes the possibility that the animal could have been an active leaper, either arboreal or terrestrial. Among living monkeys it is closest to the gelada, but is tending towards the form seen in terrestrial Carnivora like the dog.

The humerus has a poorly-developed epicondylar flange, an indication that Mm. brachialis and brachioradialis were relatively weak as they are in the gelada and *Papio;* in *Mandrillus* and the large macaques the muscles and flange are much larger. The reduction of the elbow flexors in the baboons may be related to the fact that in ground-walking powered flexion of the joint occurs only during the recovery phase, when the flexors are acting merely against the weight of the forearm and hand, and so require no great power. In climbing, on the other hand, powered flexion also occurs during the propulsive phase, during which the whole body-weight is being lifted (Jolly, 1965), thus favouring large flexors in arboreal forms. The high Index of Articular Breadth seen in Kanjera *Theropithecus* and extant baboons is largely an expression of the relatively small size of the medial epicondyle in these forms, which perhaps, can be related to the relatively small size of the mass of flexor musculature, especially digital flexors, which originates from it (Table 15). Possibly the backwardly-folded medial epicondyle of the more terrestrial forms contributes to the stability of the elbow-joint when the forearm is in its habitual pronated position.

TABLE 15

Weights of muscles originating from epicondyles of humerus (in grammes, after dissection and saturation in 10% formalin solution)

	Theropithecus gelada	*Papio I*	*Papio II*	*Mandrillus sphinx*
Radial Epicondyle				
Ext. carpi radialis brevis	8·5	4·5	4·5	22·0
Ext. digitorum communis	6·5	4·0	4·0	18·0
Ext. digit. IV et V	2·0	1·5	1·5	5·5
Ext. carpi ulnaris	5·5	3·0	3·5	15·0
Supinator	3·0	3·0	3·0	11·5
Total, Radial Epicondyle	25·5	16·0	16·5	72·0
Ulnar Epicondyle				
Flex. carpi ulnaris	12·5	11·5	12·0	31·5
Palmaris longus	3·0	3·0	2·5	10·5
Fl. carpi radialis + Fl. dig. sublimis	18·0	15·5	15·0	81·5
Pronator teres	5·0	5·0	5·5	21·5
Total, Ulnar Epicondyle	38·5	35·0	35·0	145·0

The backward inclination of the olecranon process of the ulna is a very consistent 'baboon' feature that is also seen in non-primate terrestrial quadrupeds. It also occurs, unlike some other indications of terrestrial life, in *Mandrillus*. Functionally, it can be related to the action of the M. triceps brachii, whose three heads converge to insert by a common tendon on the tip of the olecranon. As the sole extensor of the elbow, the triceps group performs two functions during the propulsive phase of locomotion, whether climbing or on a level surface. While the limb is being powerfully retracted by its extrinsic musculature, and hence is acting as a propulsive lever (Gray, 1943), it must resist forces tending to flex the elbow. Then, during the final part of the propulsive phase, it gives a powerful axial thrust to the limb by extension of the elbow, the limb then acting as a propulsive strut, in Gray's terms. The crucial difference is that in level-surface locomotion the triceps is acting upon an elbow that is almost in full extension, while in climbing the elbow is rather strongly flexed throughout the movement, presumably in order to keep the centre of gravity of the animal close to the support. The triceps is obviously at its greatest mechanical advantage when its line of action is furthest from the axis of the elbow joint, that is, when it is perpendicular to the axis of the olecranon process. The greater the inclination of the olecranon, the higher the angle between arm and forearm corresponding to this position of maximum advantage (Fig. 27). Hence, the backwardly-inclined olecranon of the baboons is most advantageous in level-surface locomotion. The evidence thus suggests that the Kanjera *Theropithecus* was at least as terrestrial as extant *Papio*, and probably as ground-living as the gelada.

The Olorgesailie form shows the same characters of humerus, ulna and femur as the Kanjera. In addition, there is evidence of extreme terrestrial adaptation in the foot bones.

Among living Cercopithecinae it was found that the more ground-living the species, the shorter and stouter its proximal and middle phalanges of digits II–V, in both the hand and the foot. In Fig. 15 the robusticity of manual and pedal proximal phalanges is expressed by plotting their breadth against their length. In spite of the fact that phalanges of all digits except hallux and pollex are included, there is a clear progression in relative shortness almost without overlap, from the arboreal genera *Cercopithecus* and *Cercocebus* through *Macaca, Mandrillus* and *Papio* to the extremely terrestrial gelada. The phalanges of Pleistocene *Theropithecus* are even more stubby than those of its living relative. A second complex of features in the foot which is

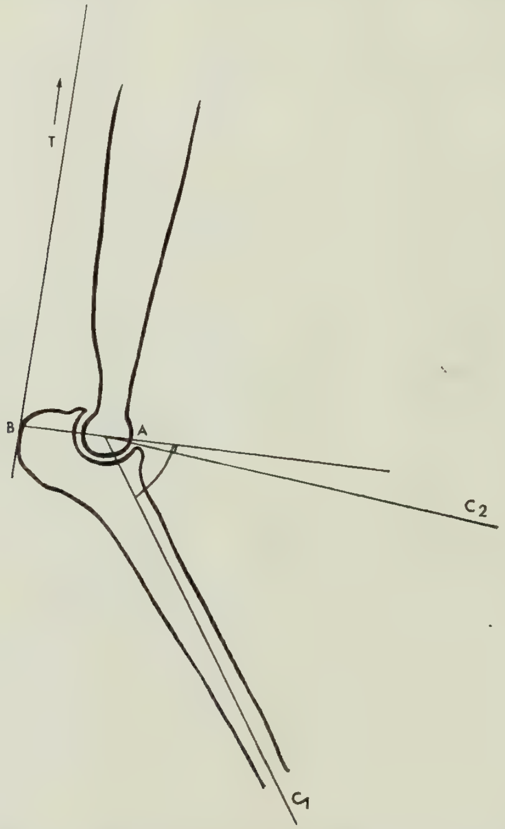


FIG. 27. Olecranon angulation and triceps action. Diagrammatic sagittal section through elbow. A. Centre of rotation of elbow joint. B. Midpoint of insertion of triceps tendon. T. Line of action of M. triceps. Triceps is at maximum mechanical advantage when angle ABT = 90°. AC_1 represents the corresponding position of the forearm in a terrestrial form with olecranon angle of about 60°; AC_2 the equivalent in an arboreal form with olecranon angle of about 10°.

related to arboreal or terrestrial adaptation concerns the relative size of the hallux and the muscles which power its movements, and its degree of abductability, all of which are greater in tree-climbing than terrestrial monkeys (Pocock, 1925, Midlo 1934, Gabis 1960; Jolly 1965). Unlike the proportions of the phalanges, the relative development of the hallux is evidently dependent upon the absolute size of the animal, as well as upon its degree of arboreal adaptation. Thus, the largest and most powerful halluces in the Cercopithecinae are to be found in the larger monkeys such as *Mandrillus* and *Macaca nemestrina* which are in other ways only moderately adapted to tree-climbing. Among animals of approximately equal body-size, the size and power of the hallux is proportional to degree of arboreal adaptation; thus, *Mandrillus* has a larger and more powerful hallux than *Papio*, and *Papio* than *Theropithecus*, and a similar relationship is seen between *Cercopithecus* and *Erythrocebus*.

Reduction in hallucial size, abductability and power in the baboons, especially in *Theropithecus*, is expressed in a variety of characters of the hallux itself, the structures in the tarsus which support it, and the relative size of the muscles which move it. The hallucial metatarsal itself is small and weak, as compared with the axial metatarsals III and IV about which the terrestrial foot is organized. The distal articular surface of the first cuneiform, which supports it, is relatively small and thus scarcely extends as a 'beak' dorsal to the body of the bone (Fig. 28). In turn, the articular facet on the second cuneiform that articulates with the 'beak' is itself small (Fig. 12) as is the superior of the two facets on the medial face of the base of the second metatarsal, which has a similar function. In the gelada (though not *Papio*) the distal articular facet of the first cuneiform scarcely extends on to the medial surface of the bone, indicating some loss of abductability of the first metatarsal (Fig. 28).

Each of these skeletal characters is observable in the *Theropithecus* material from Olorgesailie, and the shape of the distal facet of cuneiform I is as restricted as it is in the gelada.

The weakness of the baboon hallux, especially that of the gelada, was reflected in the size of the muscles powering its movement in the small series of specimens

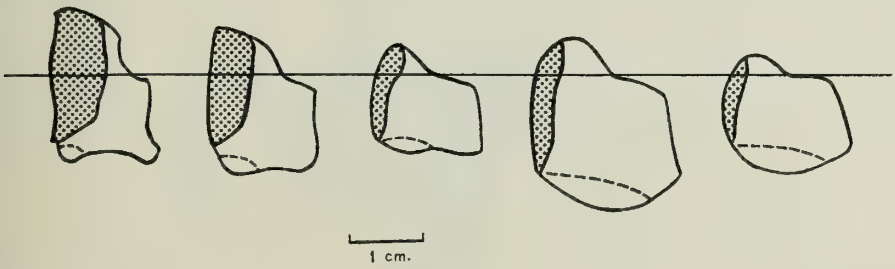


FIG. 28. Right medial cuneiform, medial aspect. Left to right: *Mandrillus leucophaeus*, male; *Papio anubis*, male; *Theropithecus gelada*, male; *T. oswaldi mariae* (2). Note: a. Relative size of distal articular surface, and its extension on to the medial aspect. b. Relative size of dorsal 'beak' (above horizontal line). Area of attachment of M. tibialis anterior tendon within dotted line.

dissected. Both the major Mm. peronei (M. peroneus longus and M. peroneus brevis) are, in the Cercopithecinae, plantarflexors and evertors of the foot. M. peroneus longus, inserting into the lateral side of the base of the first metatarsal, is in addition a powerful adductor of the hallux at the metatarsal-cuneiform joint. In the gelada M. peroneus longus was slightly less in weight than M. p. brevis. In *Papio*, longus was twice as massive as brevis, while in *Mandrillus* it was three times as heavy, reflecting closely the relative size of the hallux in the three forms. A similar relationship is seen in the antagonists of the peronei, the two parts of M. tibialis anterior. In the monkeys dissected, as well as in the rhesus monkey (Howell and Straus, 1933) the two parts were almost completely separable. Both originated from the lateral surface of the tibia and the adjoining part of the interosseous membrane. Each gave rise to a tendon passing beneath the transverse crural ligament. The tendon of the larger part of the muscle inserted upon the plantar and medial surfaces of the first cuneiform, into a prominent tubercle immediately posterior and inferior to the distal articular surface. The tendon of the lesser portion followed a similar course, but inserted into the medial side of the base of the first metatarsal. Both parts are so placed as to be dorsiflexors and invertors of the foot. The lesser portion (sometimes termed M. abductor hallucis longus) is also in a position to produce abduction of the first metatarsal, as the particular antagonist of the M. peroneus longus. As might be expected, the M. abductor hallucis constituted a greater fraction of the total tibialis anterior mass in those forms with the largest hallux, while its relationship to its antagonist was rather constant throughout the series (Table 16).

The proportions of the major peronei and the parts of tibialis anterior cannot, of course, be directly observed in *Simopithecus*, but several details of the tarsus and metatarsus indicate that these were much as in the gelada, or even more extreme. A small peroneus longus is indicated by the absence of a large tubercle of attachment on the base of metatarsal I, and even more clearly by the relatively small facet for the peroneus longus sesamoid on the cuboid. On the other hand, a large peroneus brevis is indicated by the massive peroneal tubercle on the base of metatarsal V. There is no direct evidence for a small abductor hallucis longus, but the peculiar convexity of the inferior border of the first cuneiform (which was not seen in any of

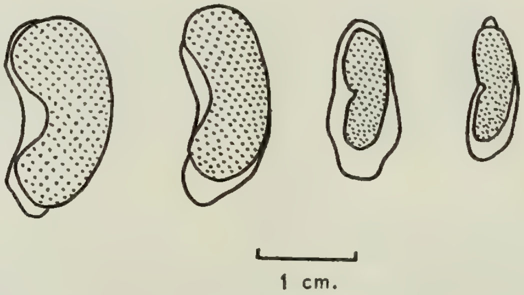


FIG. 29. Right medial cuneiform, distal aspect. Left to right: *M. leucophaeus*, male; *P. anubis*, male; *T. oswaldi mariae*; *T. gelada*, male.

TABLE 16

Weights of two parts of M. tibialis anterior and of the two major peronei (in grammes, after dissection and uniform saturation in 10% formalin)

	T. gelada	*Papio I*	*Mandrillus sphinx*
Tibialis anterior			
Major part	8·5	14·0	19·5
Abductor hallucis longus	1·5	3·0	7·5
Total	10·0	17·0	27·0
Peronei			
P. longus	4·5	8·0	20·0
P. brevis	5·0	4·0	6·5
Total	9·5	12·0	26·5
P. longus as % of total peronei	47·4	66·6	75·5
Abd.hall.long. as % of Tib. ant.	15·0	17·6	27·8
Abd.hall.long. as % of peron.long.	33·3	37·5	37·5

the 'living' series) could be interpreted as a greatly enlarged tubercle of insertion of tibialis anterior (proper).

The selectional advantage of a long and powerful hallux, and long pedal digits, to animals which habitually run along and climb branches is not difficult to find. In branch-running the transverse base of the animal is always narrow, so that the weight-line is easily displaced outside it. When this happens, a powerful turning

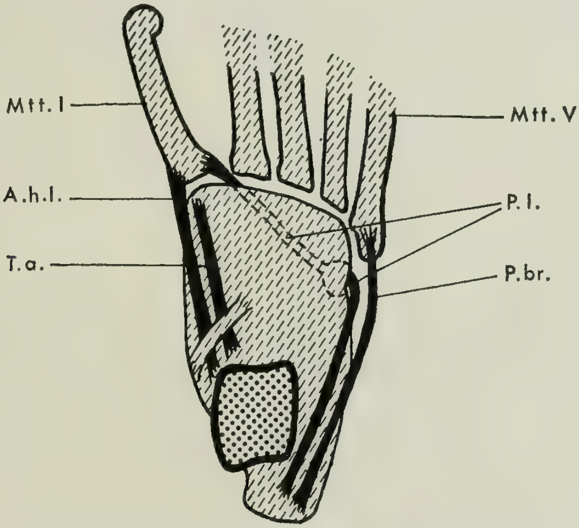


FIG. 30. Diagram of dorsal aspect of right tarsus, showing arrangement of tendons of Mm. tibialis anterior (T.a.), abductor hallucis longus (A.h.l.), peroneus longus (P.l.), and peroneus brevis (P.b.), and their insertions. Mtt. I = Hallucal metatarsal; Mtt. V = Fifth metatarsal.

couple is exerted tending to topple the animal from the branch (Fig. 31). The moment of the couple is *Wh*, where W is the weight of the animal and *h* the distance by which the weight-line is displaced. If the animal is not to fall, this couple must be resisted by an equal and opposite frictional couple exerted by the extremities, especially the feet. This frictional couple, in turn, is determined largely by the diameter of the branch spanned (*d*), and the amount of pressure that can be exerted normal to the branch surface by the action of the digital flexors and hallucal adductors (V_1 and V_2). Long phalanges in digits II–V, and a long and abductable hallux increase the possible size of *d*, while powerful flexors of the digits and adductors of the hallux increase V_1 and V_2, respectively. The apparently disproportionately large hallux of the mandrill and other big, semi-arboreal monkeys, can be accounted for by the fact that while *d* is increased as the length of the hallux and other digits, W increases as the *cube* of linear body-dimensions. Thus, the hallux needs to be long relative to general body dimensions. In ground-walking and running, on the other hand, a long, abducted hallux and long digits would be of little value, and probably in fact a positive handicap.

It is quite clear that the Olorgesailie *Simopithecus* most closely resembled the highly terrestrial gelada in those characters of the foot which are good indicators of

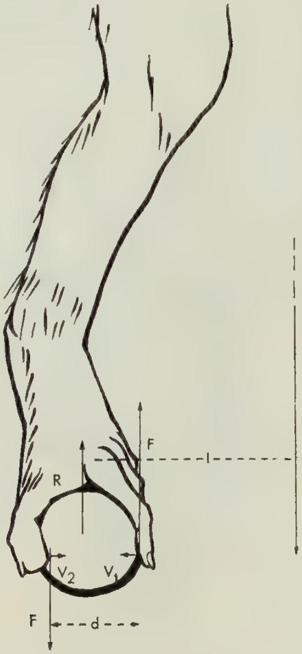


FIG. 31. Forces acting upon a foot gripping a horizontal branch with the hallux, when the animal's weight-line is displaced beyond the branch. (Modified after Gray, 1943).

arboreal/terrestrial adaptation. Bearing in mind that larger monkeys need relatively longer halluces than smaller ones of the same degree of arboreal adaptation, it is particularly striking that a *Theropithecus oswaldi mariae* male, an animal perhaps the size and weight of a female gorilla, had a hallux no larger than that of a mandrill, a semi-arboreal animal weighing only about one-third as much, and could not have obtained a foothold on branches more than about 3 inches in diameter. The implication is that it could not have climbed trees or walked along branches as part of its daily routine, and probably could do so only in a clumsy manner in an emergency or for a night-refuge. Of course, the short, stout digits and weak hallux would be no handicap to an animal which climbed crags or rock-faces, as does the living gelada, and it is possible that *Simopithecus* was also dependent upon such places for night-refuges. In this case, however, its environmental requirements (both permanent, fresh water and crags within its daily range) would be more demanding than is indicated by its wide range and common occurrence in fossil faunas. Alternatively, it is possible that the larger *Simopithecus* roosted on the ground, relying on their strength as a defence against predators, in the same way as living male gorillas.

The Olduvai II *Simopithecus* evidently had digits that were as short and stout and a hallux as reduced, as those of its descendants at Olorgesailie (Fig. 15), a clear indication that it, too was a ground-living animal. The evidence of the humeri, with rather large and projecting brachioradialis flanges and stout ulnar epicondyles, seems rather to indicate an animal with powerful elbow and digital flexors, and hence a semi-arboreal way of life. There are two possible explanations for this apparent inconsistency; either the humeri belonged to another large cercopithecoid, not *Theropithecus*, or else the *Simopithecus* line was still in process of adaptation to full terrestrial life during the early Middle Pleistocene, and, having acquired the short digits of a ground-living monkey, had yet to lose the large flexors of a semi-terrestrial form.

We have no information about the postcranial skeleton of the remaining *Simopithecus* forms.

C. Adaptations to diet in the Dental and Cranial Anatomy of *Simopithecus*

In section V we determined the trends in dental and gnathic evolution which distinguish *Theropithecus* from other large Papionini. It is possible to interpret these characteristics as a single, diet-related functional complex. Observations of living animals indicate that the dentition of Cercopithecoidea may be considered in terms of three functional regions: incisors, cheek-teeth, and canines + P_3. The *incisors* are mainly used in the preliminary processing of food-objects as these are held in the hand, more specifically for separating the edible portion from the inedible, which is then discarded. Tasks in this category include biting through the husks of fruits, nibbling the flesh of fruits from the rind, and, occasionally, the meat of mammals or birds from the skin or bones, and stripping or plucking buds, leaves or small fruits from a stem or branch as it is drawn between the teeth. Quite often, especially in the case of leaf-eating Colobinae (Ripley, 1970) the branch is not broken off before being brought to the mouth for stripping, and occasionally the incisors are used to prise a closely adherent food-object from an immovable substrate. They are however, not used in a manner analogous to the grazing of ungulates, to pluck small, easily picked food objects from the ground or other fixed substrate; such objects are invariably picked up by hand, or, occasionally, with the lips or tongue. The small incisors characteristic of *Theropithecus* suggests that such preparatory activities are a relatively unimportant part of its feeding habits, and thus that its diet includes a relatively minor proportion of items requiring preparation before mastication. This is consistent with the known diet of *T. gelada*, which consists very largely of small objects which are gathered by hand and placed in the mouth whole. The diet of *Papio*, on the other hand, especially in the overlap zone, includes a high proportion of items, largely tree-products, requiring such preliminary preparation (Crook and Aldrich-Blake, 1968), and the rapid wear to which the incisors, though large, are subject, is attested by wild-shot skulls.

The *premolars and molars* (apart from P_3) are concerned with trituration of the food mass after preliminary preparation, if any. The movements involved have yet to be fully elucidated by cineradiography, but appear to be mainly lateral (Mills, 1963). In *Theropithecus*, the amount of occlusal surface available for this function is very large, relative to body-weight as compared to, for instance, *Papio*. For example, in a sample of nine males of *Papio ursinus ursinus* (Jolly, 1965) the mean 'area' of the upper cheek teeth (sum of length × breadth) is 568 cm^2; in the *T.* (*S.*) *oswaldi oswaldi* male, an animal of closely comparable bulk, it is 868 cm^2. This feature indicates a diet in which the major food items are tough and therefore require extensive chewing to break them down, or low in nutritional value per unit volume, so that large quantities must be processed. Both these attributes apply to the predominant foods of *T. gelada*, which has been observed to spend a greater proportion of its time than other baboons in feeding (Crook and Aldrich-Blake, 1968).

In all Cercopithecoidea, the molars and premolars show high relief in their crowns, as compared to Hominoidea, among which only the gorilla approaches the condition normal in the monkeys. In Colobines and *Theropithecus* however, occlusal relief is further exaggerated in association with a diet which (like that of *Gorilla*) includes a high proportion of the vascular parts of plants. In Colobinae, the major cusps are linked by high cross-lophs, and there is a tendency to reduce structures mesial and distal to the principal cusp-pairs. The effective surface is therefore made up of a series of sharp transverse ridges, upper interlocking with lower, a pattern which persists until an advanced stage of wear, and is presumably related functionally to chopping foliage. In the molars of *Theropithecus*, extreme crown height and relief is associated with *additional* clefts and fossae, especially mesial and distal to the major cusps, with the formation of a prominent *longitudinal* ridge, and with a wear pattern in which the occlusal surface of the molar crown is reduced to a plane surface at an early stage. Clearly a different adaptive pattern is involved, in which the grinding surface is provided by the pattern of enamel ridges, the remains of the walls of the cusps and the inter-cusp crests, which project from exposed dentine in the worn tooth-surface. When wear is advanced, the only relief is provided by 'studs' of enamel which originally formed the floor of the deepest inter-cusp hollows.

With these gone, the molar must be considered virtually useless for grinding, having only a continuous dentine surface.

The adaptive advantage of the *Theropithecus* molar over the bunodont *Papio* type is first that, the greater complexity of invaginations provides more enamel ridges on the surface of a worn tooth; second, that the more parallel-sided and deeper inter-cusp clefts and basins prolong the presence of these enamel ridges to a more advanced stage of wear, and third, that the high crowns provide more material to be abraded and thus postpone dental obsolescence still further. This functional pattern accords well with the graminivorous diet of *T. gelada*; grasses, by virtue of their siliceous cell-coats are resistant to digestion, and thus require fine trituration before swallowing to release their nutrients. For the same reason, and because of the soil particles which are likely to be ingested with them, they are extremely abrasive.

The hypothesis that this type of molar is adaptive to a diet consisting largely of grasses is supported by the fact that cheek teeth with high crowns, more complex ridging, and columnar shape accompany grazing habits in mammals as diverse as Perissodactyls (Equidae), ruminant Artiodactyls (Bovidae etc.), Suidae (*Phacochoerus* and allied forms), Proboscidea (Elephantidae) and Rodentia (Microtinae).

As noted previously there is some evidence that in the subgenus *Simopithecus*, at least, the third molars tended to come fully into occlusion late, relative to the first molars and to the anterior teeth, especially the male canine. It is impossible to tell, from fossil material, whether this represents merely a modification of eruption within a period of dental development that was no longer in total than the cercopithecoid norm, or whether the third molars erupted later in the life of the animal. Whether relative or absolute, however, the delayed eruption of M_3 would seem to represent an adaptation combating heavy molar wear, by replacing and crowding forward worn-out anterior molars, while retaining the mechanically advantageous short dental row. This would not be possible if all three molars were present and in occlusion in their unworn condition. Again, there is a parallel to grass-eating mammals of other orders, notably horses and elephants.

The *canines* of Cercopithecoidea (together with the anterior face of P_3, which functionally belongs with them) are used in fighting rather than feeding. The tendency towards reduction of canine height in males, characteristic of subgenus *Simopithecus*, was, however, probably dietary in origin. As in other Anthropoidea apart from Hominidae, the occlusal plane in worn molars and premolars of *Theropithecus* is inclined buccally, the lingual cusps of the upper teeth, and the buccal cusps of the lower, sustaining the heavier wear. This asymmetry is clearly related to the projecting crown of the upper canine which limits horizontal movement during the lingual phase of chewing by coming into contact with the 'honing' face of P_3. In female Cercopithecinae, the canine tip not infrequently wears to the level of the crowns of the other teeth, and a flatter wear-plane is produced in the post-canine region. In males, however, except in rare individuals, the canines, although they may become worn and often broken, continue to project, maintaining asymmetrical wear on the cheek-teeth, throughout life. In these cases, final obsolescence of the individual cheek-tooth occurs with the breakdown of the enamel wall of the more severely worn side, lingual in the upper teeth, buccal in the lower. In *Thero-*

pithecus with its back-tooth dominance and abrasive diet, prolongation of the life of the molars and premolars was clearly at a special evolutionary premium, and two adaptations appear to have arisen to meet the challenges of canine-induced asymmetrical wear. First, the additional height added to the tooth-crown as hypsodonty evolved was allocated more heavily to the side of the crown subject to the heavier wear in life. The resulting asymmetrical hypsodonty, with crowns higher on the lingual side in the upper teeth, and the buccal in the lower, is characteristic of both subgenera of *Theropithecus*. The second adaptive trend seen clearly only in *Simopithecus* was to reduce the height of the male canine. This probably had little effect upon molar wear during its early stages, but would raise the probability of the canine's wearing flat before the collapse of the molars, thus prolonging their life (and that of the animal), by allowing a period of symmetrical wear. The predictable end-point of such a trend would be a condition like that in early Hominidae, where the canine crown projects so little when unworn that it invariably wears to the level of neighbouring teeth, and permits symmetrical molar wear, from an early stage.

Again, this hypothesis finds some support in the fact that modifications of the canine, with the effect of permitting horizontal occlusion and free lateral movement of the cheek-teeth, are practically universal in mammalian groups adapting to grazing or to other ways of life dominated by heavy chewing. Grazing pigs (*Phacochoerus* and its allies) retain but re-orient the upper canines so that they do not interlock; the various groups of pecoran and perissodactyl grazers greatly reduce or eliminate them. Among primates, reduced canine crown height is evident in the three other genera which most clearly exhibit signs of adaptation to heavy chewing: the hominoids *Gigantopithecus* and *Australopithecus* and the lemuroid *Hadropithecus* (Simons and Ettel, 1970; Jolly 1970a, 1970b).

In those groups in which canine modification has taken the form of reduction rather than re-orientation, the evolutionary problem has arisen of developing alternative means of combat and defence, and has been variously solved by the elaboration of somatic or extra-somatic weapons (antlers, horns, artefacts). Unfortunately when *Simopithecus* became extinct, its canines, though much reduced from the cercopithecoid norm, were still large and projecting enough to preclude the need for such alternative weapons.

The cranial indications of massively-developed muscles of mastication, especially pterygoids and masseter, seen in *Theropithecus* are again consistent with a diet requiring heavy molar and premolar chewing. The narrow postorbital constriction, anterior position of the union of the temporal lines and vertical orientation of the ascending mandibular ramus all attest to a temporal muscle the mass of which is more anteriorly placed than that of *Papio* or *Mandrillus*, and whose fibres are more nearly perpendicular to the occlusal plane. The deep posterior maxillae may be seen in part as a way of preserving this vertical orientation while accommodating allometric lengthening of the face. The mechanics of mastication in monkeys have yet to be analysed experimentally. However, simple geometrical relationships between the occlusal plane and the approximate resultant forces of the masticating muscles suggests a functional explanation of the *Theropithecus* pattern. Contraction of the muscle results in forces of occlusion and of retraction. The latter, when generated by bilateral contraction, are presumably involved in incisal 'nibbling', while the former, generated by alternating contraction of the musculature of either side, are synergic to the action of masseters and pterygoids in opposing the occlusal surfaces of the cheek-teeth and moving the mandible laterally in 'rotary' chewing. The orientation of the temporal in *Theropithecus*, by increasing the angle between its line of action and the occlusal plane towards 90°, increases the occlusal but decreases the retractive component of its action. Analogous variation is seen in other mamalian groups. Aside from the Carnivora, forms with the mandibular condyle set on or approaching the occlusal plane are to be found chiefly among the rodents in which incisor function is clearly dominant; significantly, *Daubentonia* and the extinct 'gnawing' Prosimii (e.g. *Plesiadapis*) also show this condition. In grass-eating animals with grinding molars, on the other hand, the mandibular condyle is set well above the occlusal plane, and as far forward as is anatomically possible, producing a vertical ascending ramus. Such a condition is seen in, for instance, the grazing horses and Artiodactyls, the elephants, and the grazing pigs. In the case of the Proboscidea (Osborn, 1936–42); and the Suidae (Ewer, 1956) there is evidence of the evolution of grazing forms with high, vertical ascending rami and hypsodont cheek-teeth from bunodont ancestors with lower rami and presumably a diet of fruits and tubers. It is tempting, therefore, to consider the vertically-oriented ascending ramus of *Theropithecus*, with which may be correlated the forwardly-set temporal muscles, as similarly adaptive to a diet consisting largely of grass.

Structures in the glenoid region – the antero-posteriorly narrow glenoid fossa, confined posteriorly by a stout post-glenoid process, the mandibular condyle with its articular surface confined almost entirely to its superior aspect – can also be plausibly interpreted as correlates of masticatory habits in which lateral chewing movements predominate.

VII. SUMMARY AND DISCUSSION

The genus *Theropithecus* seems to be derived from a primitive, African, stock of Papionini which began to exploit the open-country grassland niche not later than the middle-to-upper Pliocene. A stock of primitive *Theropithecus* probably became isolated in the Ethiopian highlands, and gave rise to the modern gelada, while the other forms continued to specialize in the lowlands. Like their living relative, the latter were inhabitants of open country, rarely if ever climbing trees, and preferred the margins of shallow lakes where seasonal flooding inhibited the growth of trees but enriched the ground-flora, especially of grasses. Blades, seeds and rhizomes of grass, picked by hand, probably supplied the bulk of the diet, but would have been supplemented by other small food-objects.

The extinction of subgenus *Simopithecus* which seems to have occurred about 50,000 years ago, requires no explanation in terms of widespread climatic change. As in the case of other large, comparatively slow-moving animals, the influence of human hunters is likely to have been a highly significant factor in the disappearance of the genus from most of its Pleistocene range. As has been emphasized elsewhere, higher primates are peculiarly vulnerable to over-hunting because of their slow reproductive rate (Jolly, 1966), which makes them dependent for survival upon a high rate of success in rearing young to maturity. The larger forms of *Simopithecus* are likely to have been even more slow-breeding than their smaller contemporary relatives. The disappearance of *Simopithecus* corresponds to a wide-ranging impoverishment of the African mammalian fauna, mainly by the extinction of larger forms (Cooke, 1963), and, significantly, to a period of diversification of human cultures and elaboration of hunting techniques (Clark, 1959, Cole, 1954). At both Olduvai and Olorgesailie there is evidence of extensive hunting; at the latter site *Simopithecus* was apparently a staple food during one period of human occupation (Isaac, 1966).

On the other hand, it would be naive to suppose that *Simopithecus* was literally exterminated by the hand of man. Rather we should see human interference as disturbing an ecological balance between it and related genera, especially *Papio*. Of the two, *Simopithecus*, slower moving, less able to escape by climbing, larger, but less well-equipped with canine teeth, probably slower breeding, and dependent upon long daily periods of uninterrupted feeding in the very lakeside habitat which was apparently the favoured hunting and gathering ground for early man, was much the more likely to be adversely affected by human predation, competition and simple disturbance. Each reverse to *Simopithecus* would have been to the advantage of sympatric populations of *Papio* baboons, whose generalized structure enables them to respond flexibly to predation and competition from humans, yet which, as their modern distribution and natural history shows, are quite capable of exploiting opportunistically those resources which primitively were the domain of *Theropithecus*, and which remain so in its refuge areas of the high Simien.

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PLATE 1

Skulls of extant Cercopithecinae

a. ***Mandrillus leucophaeus,*** male × ½
b. ***M. leucophaeus,*** female × ½
c. ***Theropithecus gelada,*** male × ½
d. ***T. gelada,*** female × ½

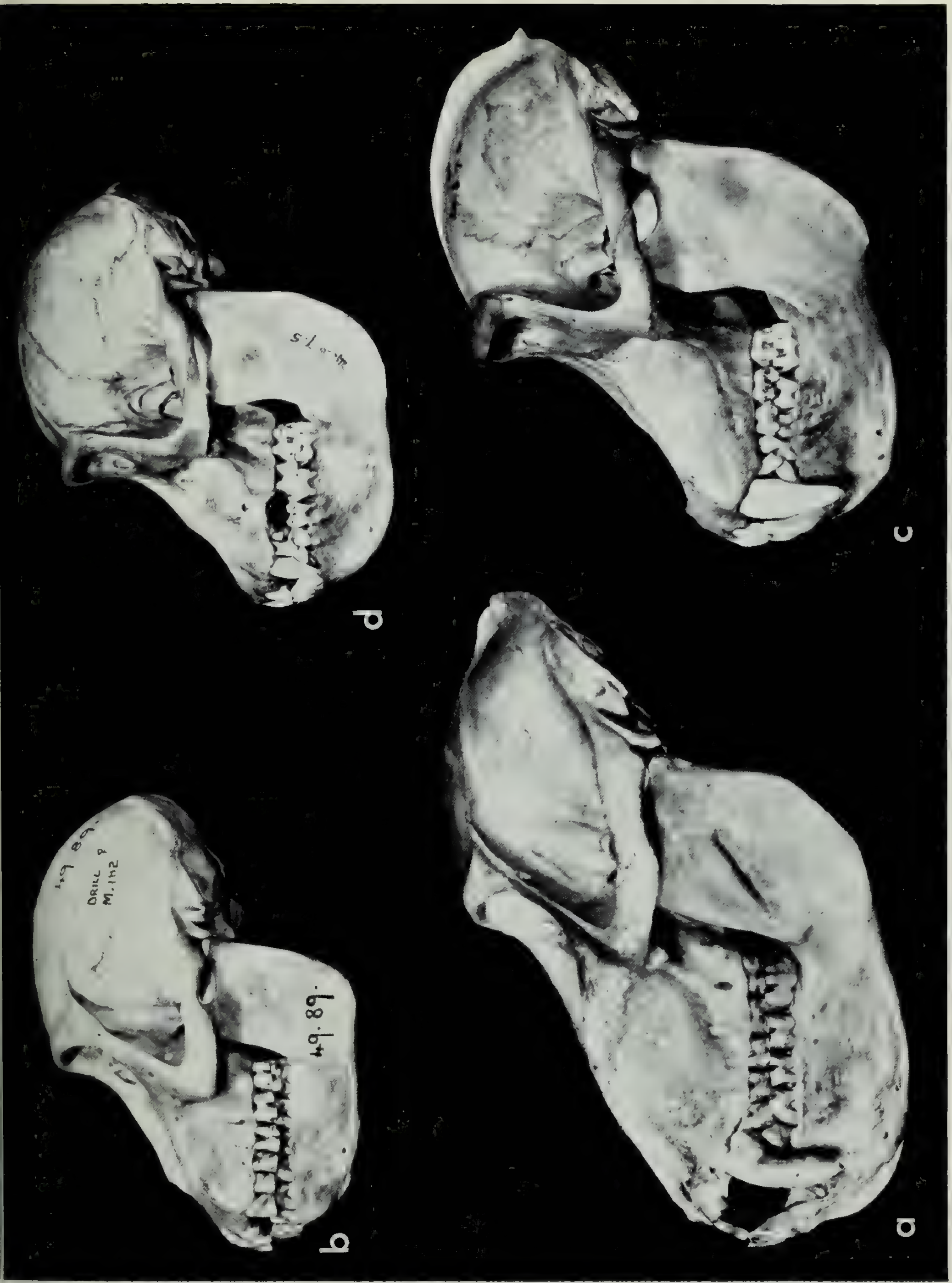

a
b
c
d
49.89.
DRILL ♀
M.142
49.89.

PLATE 2

a.	***Papio cynocephalus kindae,*** male	× ½
b.	***P. c. kindae,*** female	× ½
c.	***Papio ursinus,*** male	× ½
d.	***Papio ursinus,*** female	× ½

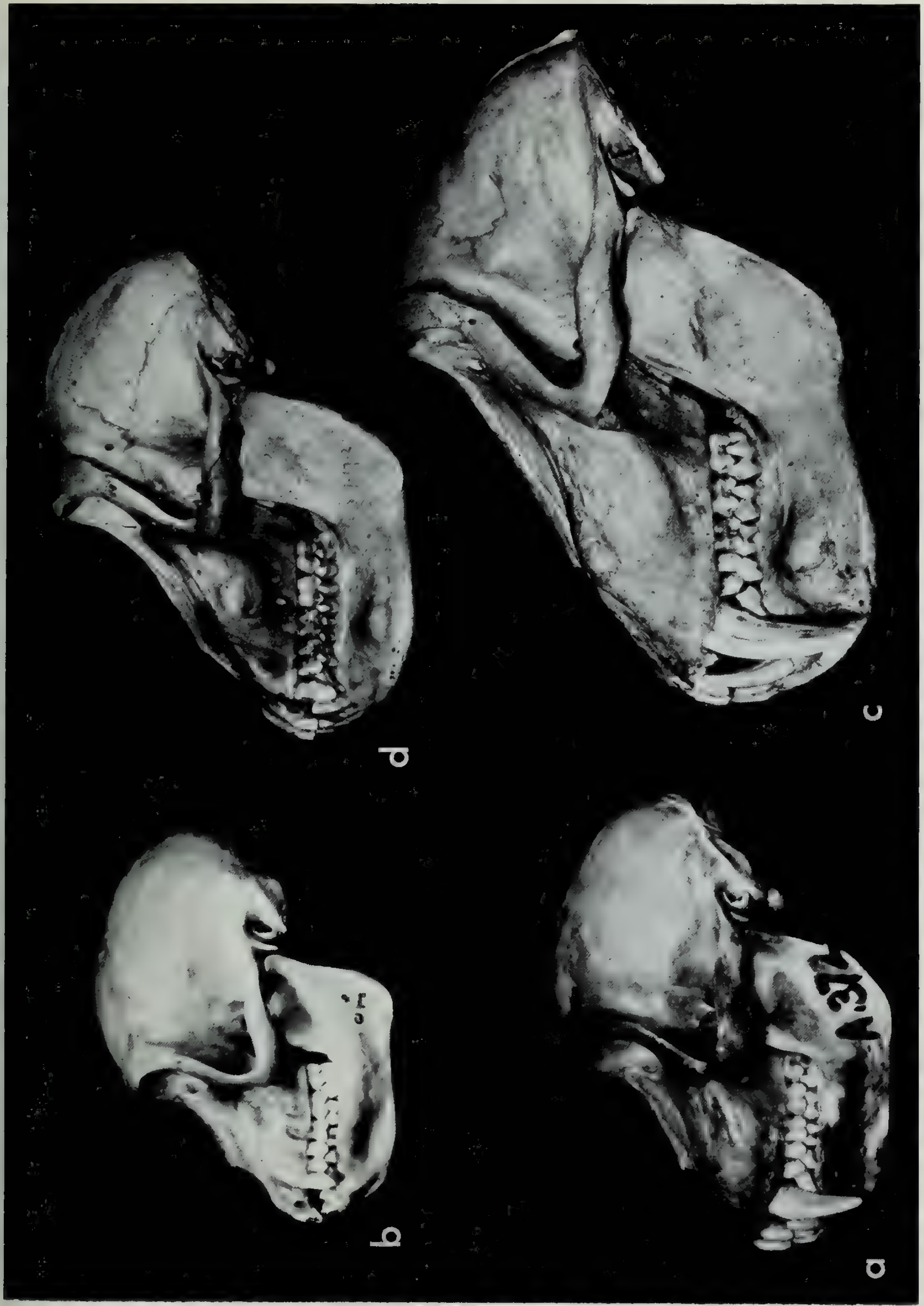

a
b
c
d

PLATE 3

Theropithecus oswaldi oswaldi

a. Male cranium, F 3668	× $\frac{1}{2}$
b. Female P_3, M 18763	× 2
c. Male P_3, M 18755	× 2
d. Female lower canine, M 18753	× 2
e. Male lower canine, M 18729	× 2

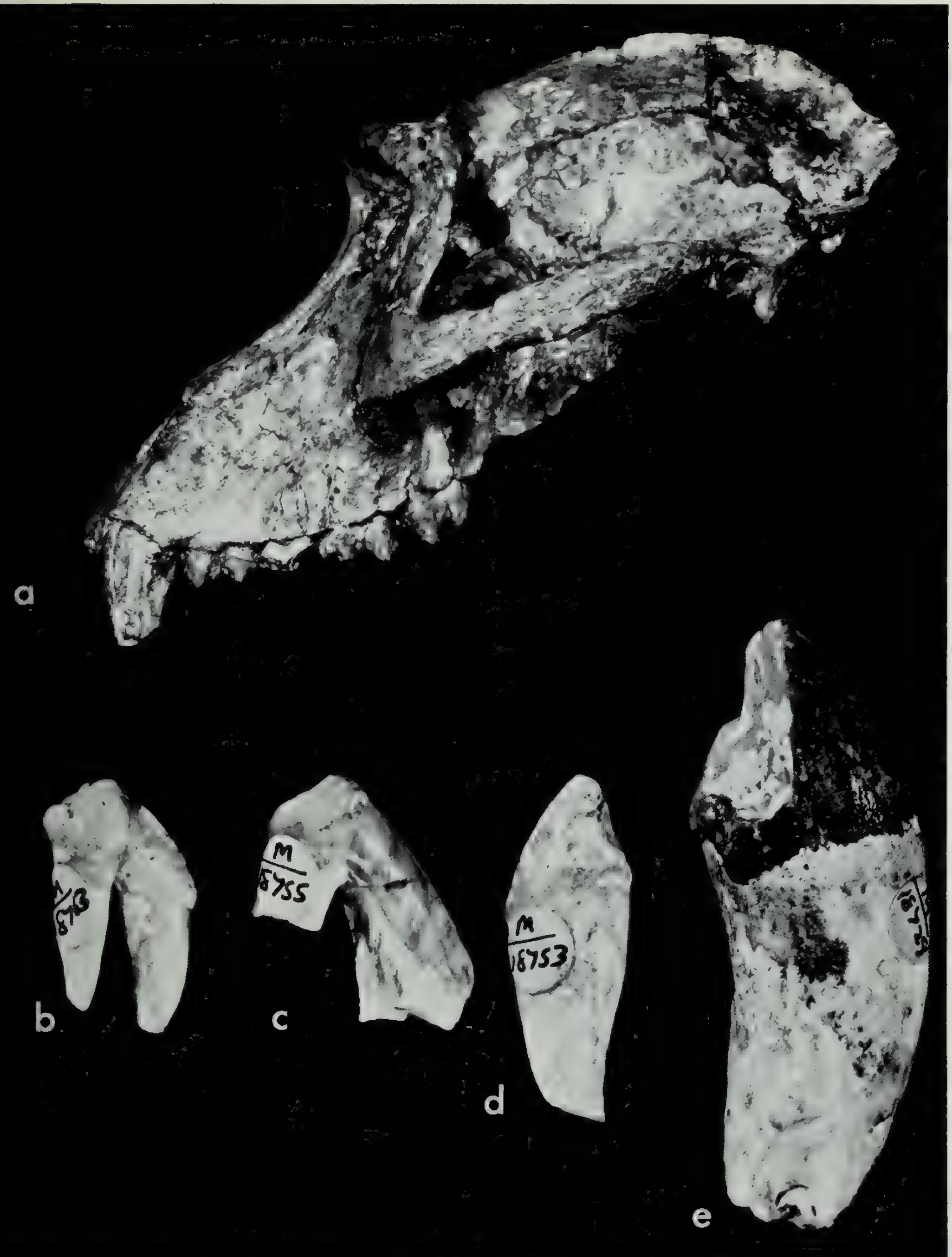

a
b
c
d
e
M
18755
M
18753

PLATE 4

Theropithecus oswaldi oswaldi

a. Male cranium, F 3668	× 2/3
b. Frontal, M 18765	× 1
c. Frontal, F 3394	× 1

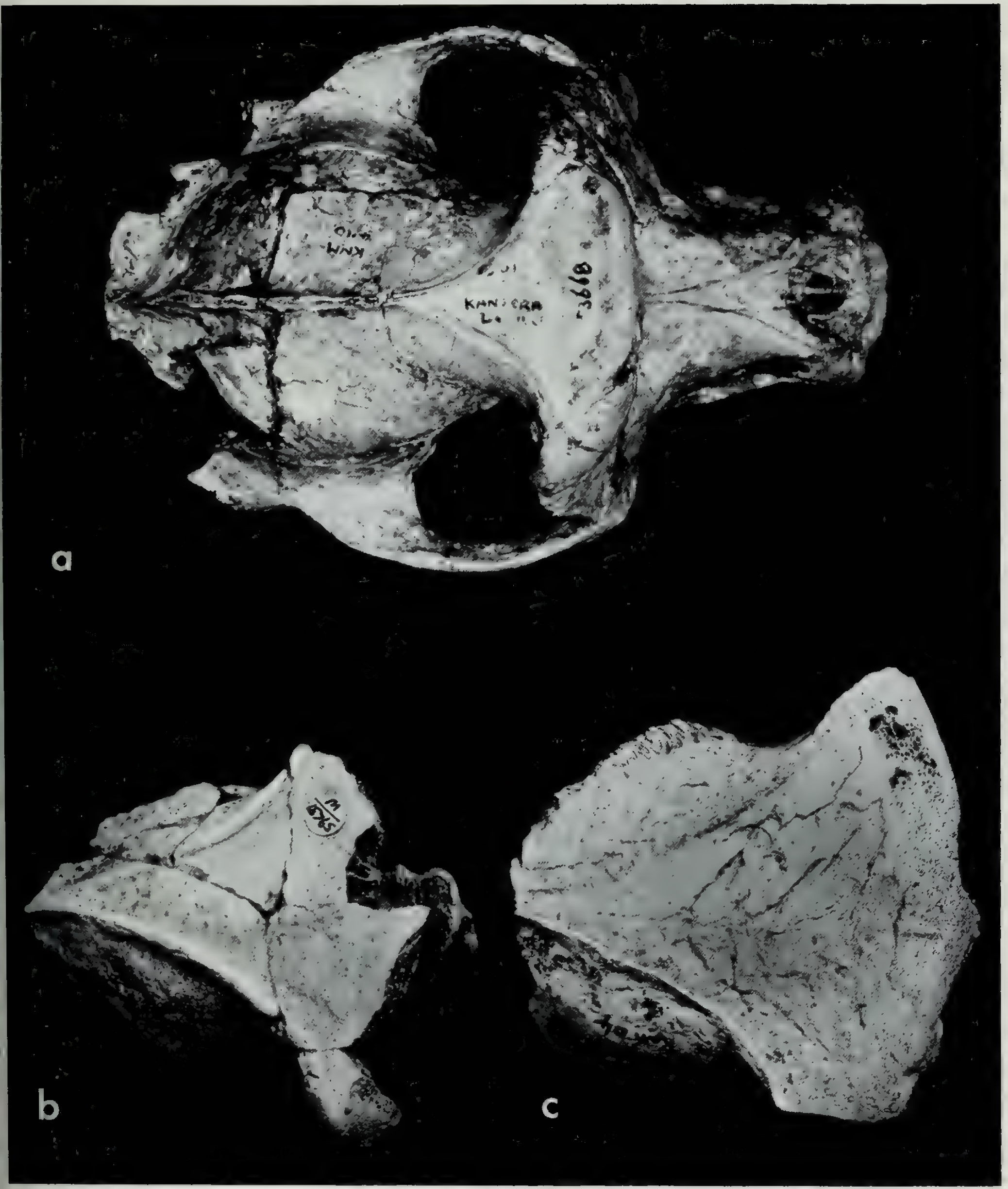

KNM
KANJERA
a
b
c

PLATE 5

Theropithecus oswaldi oswaldi

a, b. Female cranium, M 14936 × 2/3

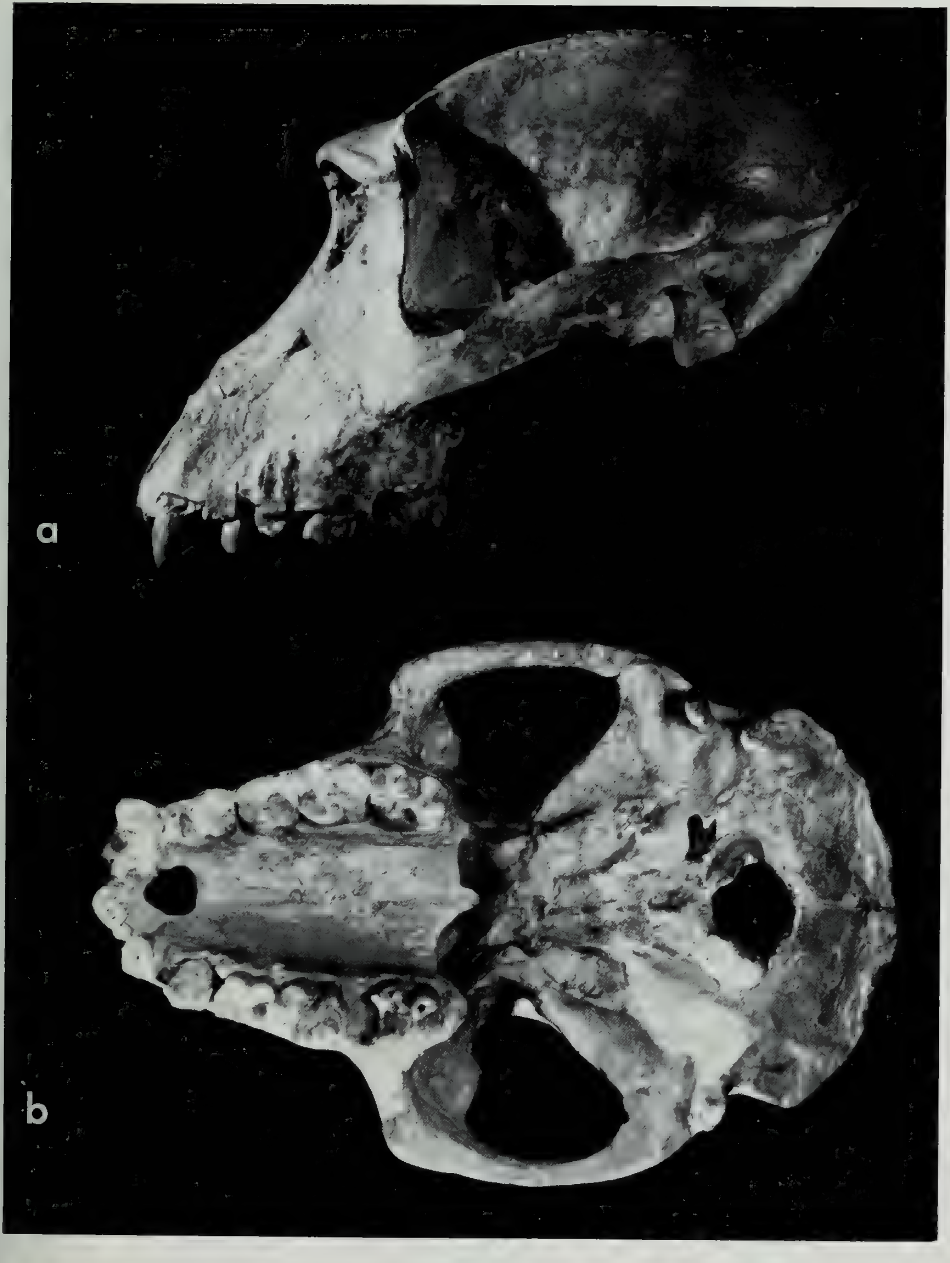

a
b

PLATE 6

Theropithecus oswaldi oswaldi Female

a. Cranium, M 14936	× 2/3
b. Maxillary dentition, M 14936	× 1
c. Anterior muzzle, M 18720	× 1
d. Cranium, M 14936	× 2/3

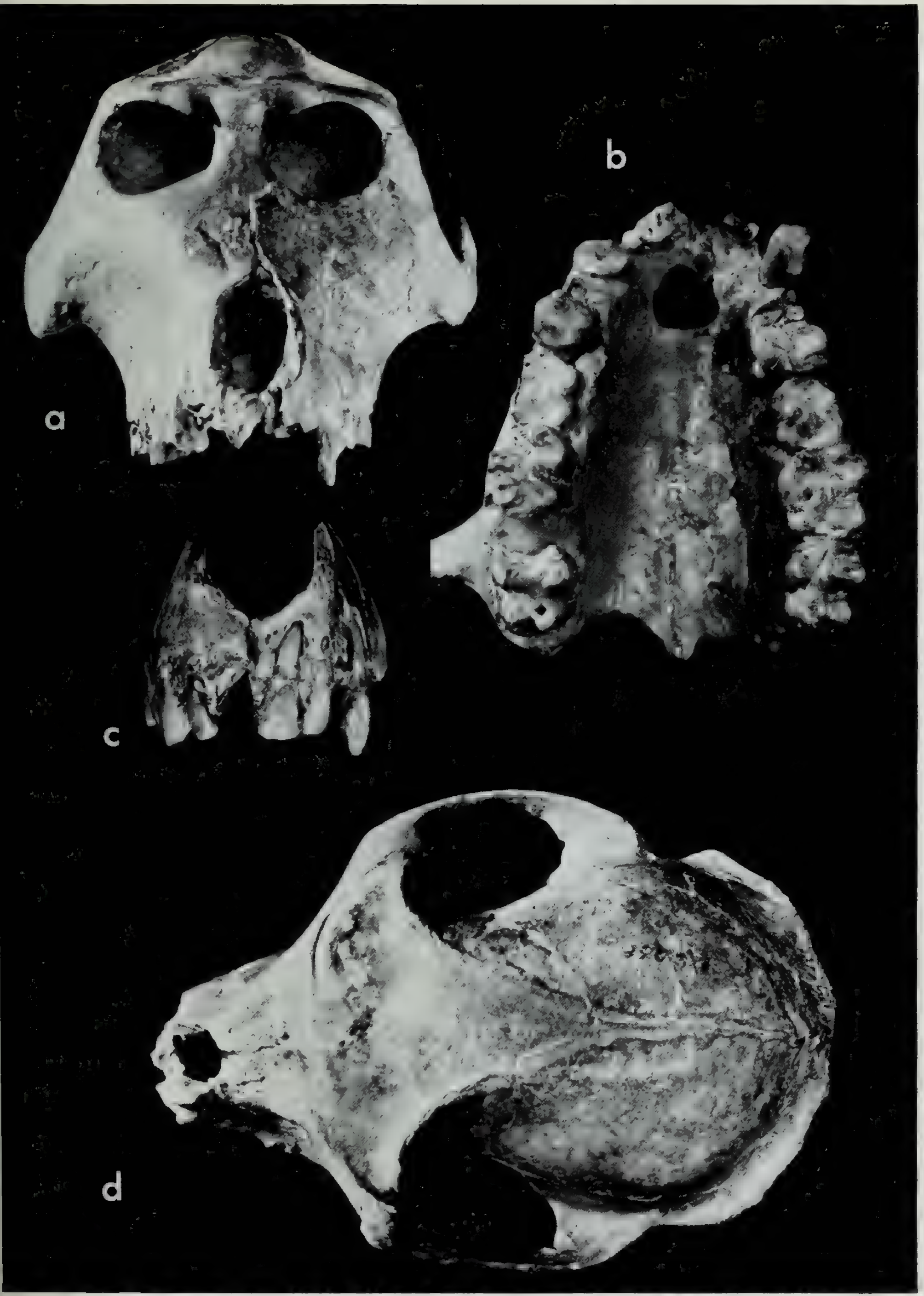

a
b
c
d

PLATE 7

Theropithecus oswaldi oswaldi Female

a. Reconstructed muzzle, M 11538 and M 18720	× 1
b. Maxillary dentition, M 11538 and M 18720	× 1
c. Muzzle, M 11537	× 1
d. Maxillary dentition, M 11537	× 1

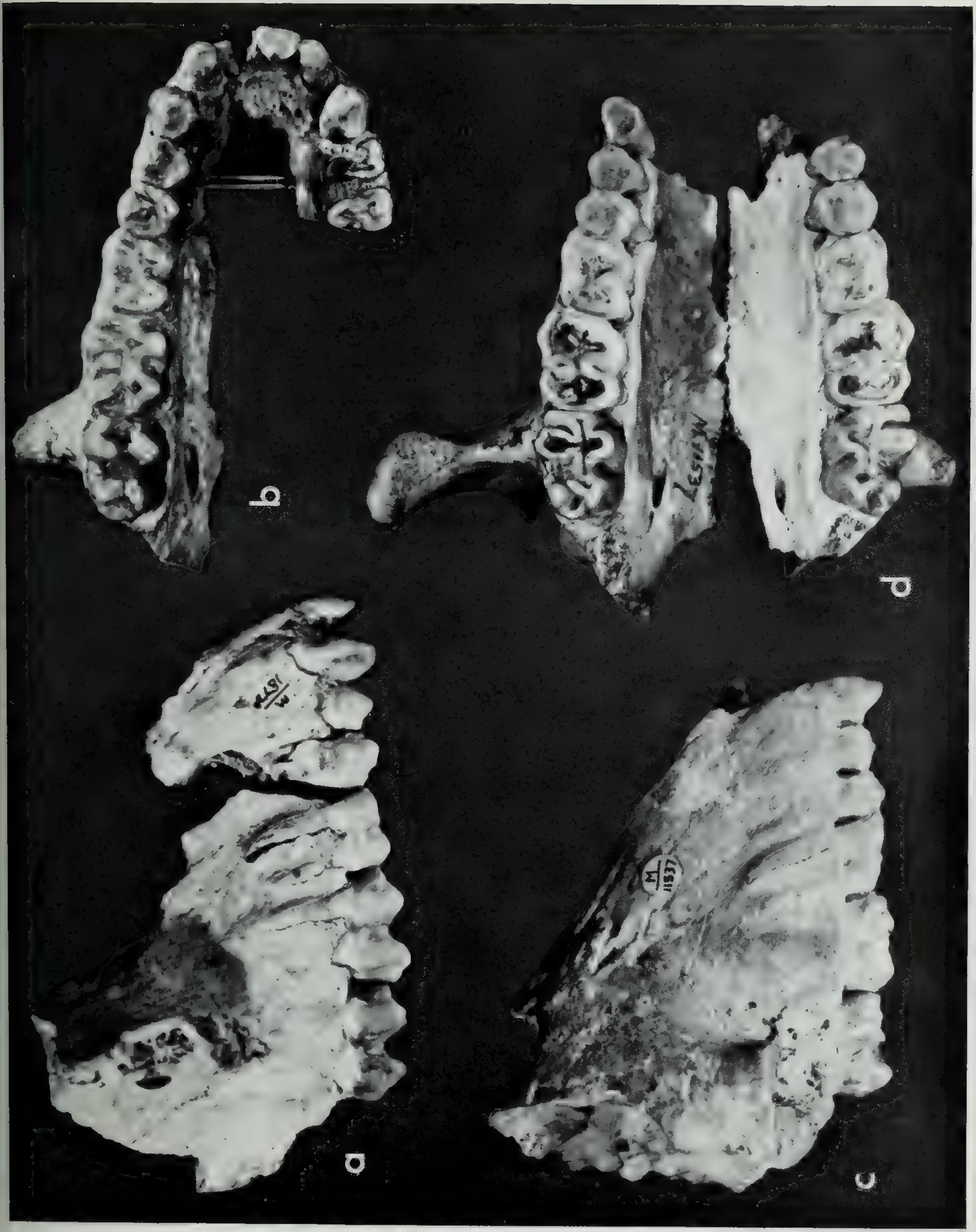

a
b
c
d

PLATE 8

Theropithecus oswaldi oswaldi

a, b. Cranial fragment, M 18764	× 1
c, d. Female mandibular fragment, M 19011	× 1

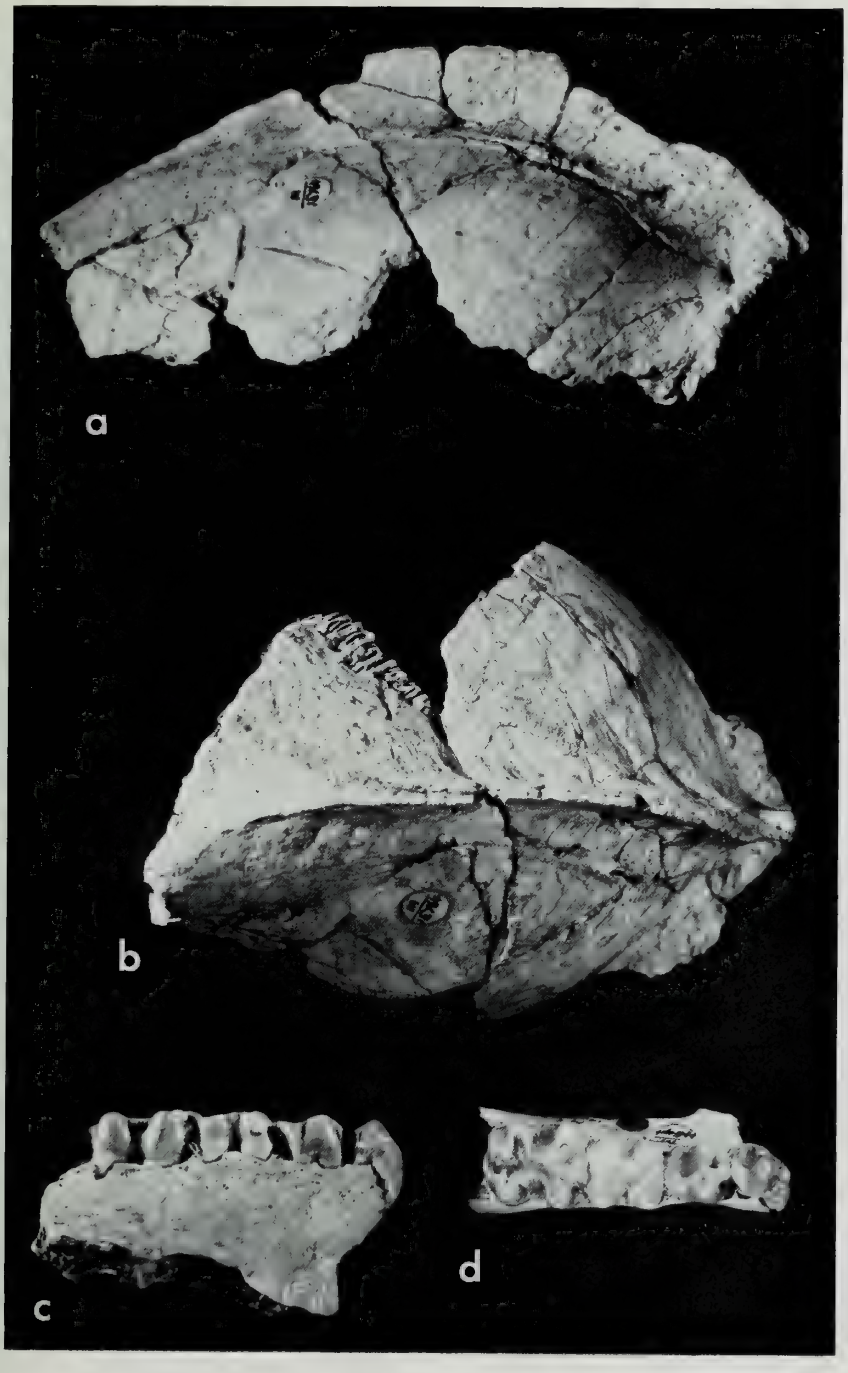

a
b
c
d

PLATE 9

Theropithecus oswaldi oswaldi

a. Mandibular fragment, probably male, M 11541	× 1
b. Female mandible, M 11539 (Type of *Simopithecus oswaldi*)	× 1
c. Juvenile female mandible, F 3398	× 1
d. M_3, light to moderate wear	× 2
e. M_3, light wear	× 2

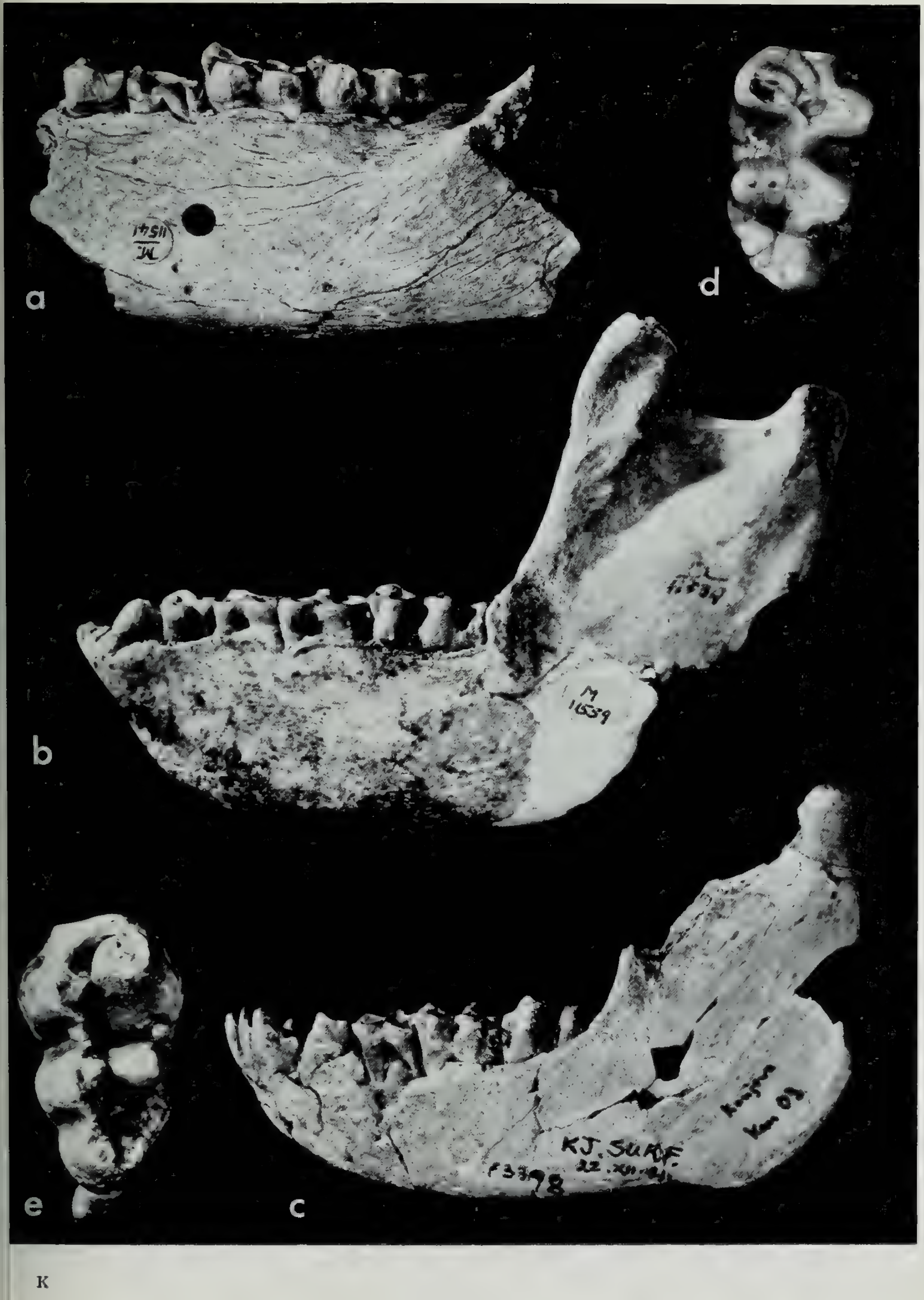

a
M
11541
d
b
M
1559
e
c
KJ. SURF.
22.XII.61

PLATE 10

Theropithecus oswaldi oswaldi

Mandibular dentitions,

a. M 11539 (Type of *S. oswaldi*)	× 1
b. F 3398	× 1
c. M 11541	× 1

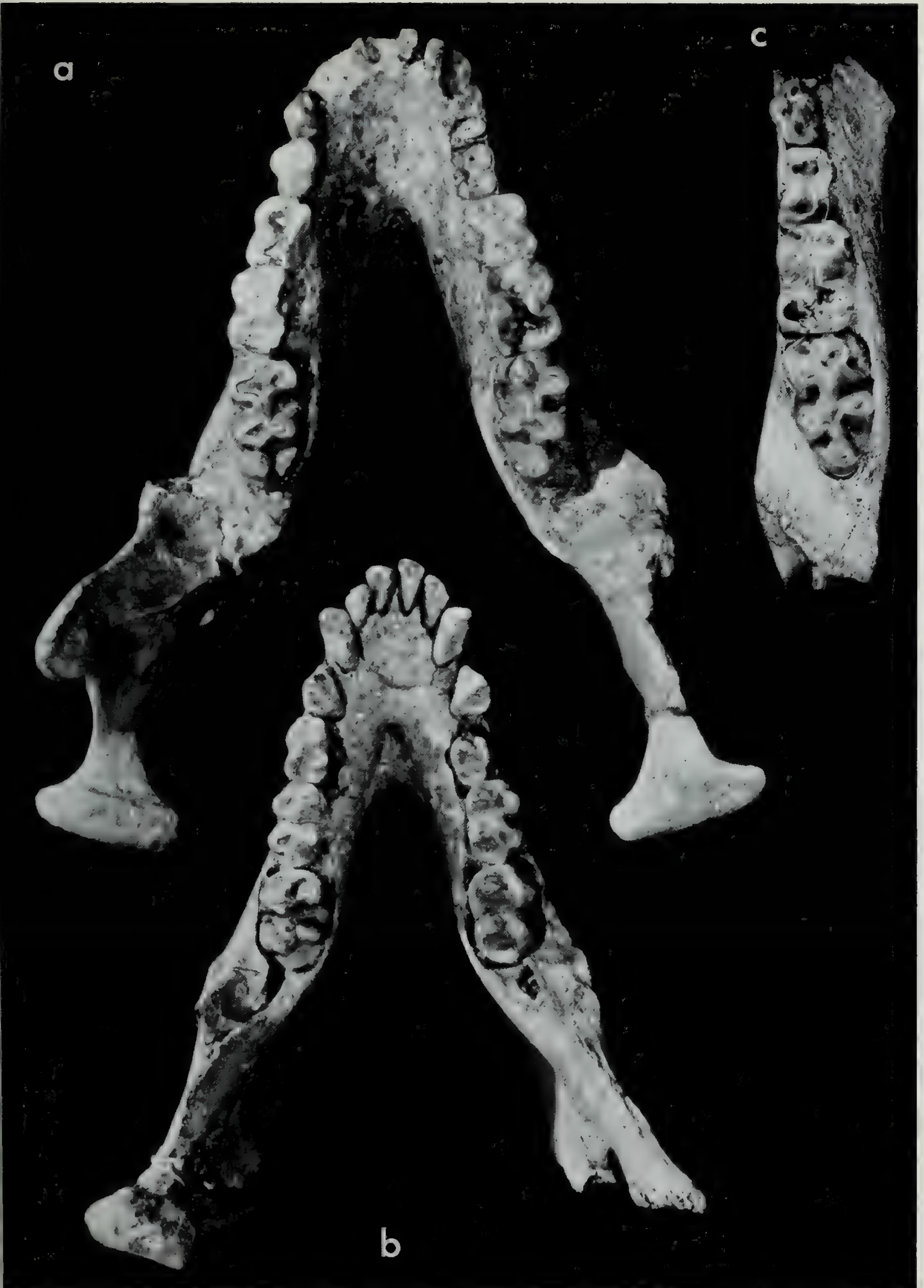

a
b
c

PLATE 11

Theropithecus oswaldi oswaldi

a, b. Scapular fragment (no. 3 in list)	× 1
c. Humeral fragment, anterior aspect, M 18789	× 1
d. Humeral fragment, anterior aspect, M 18721	× 1
e. Humeral fragment, anterior aspect, M 11542	× 1

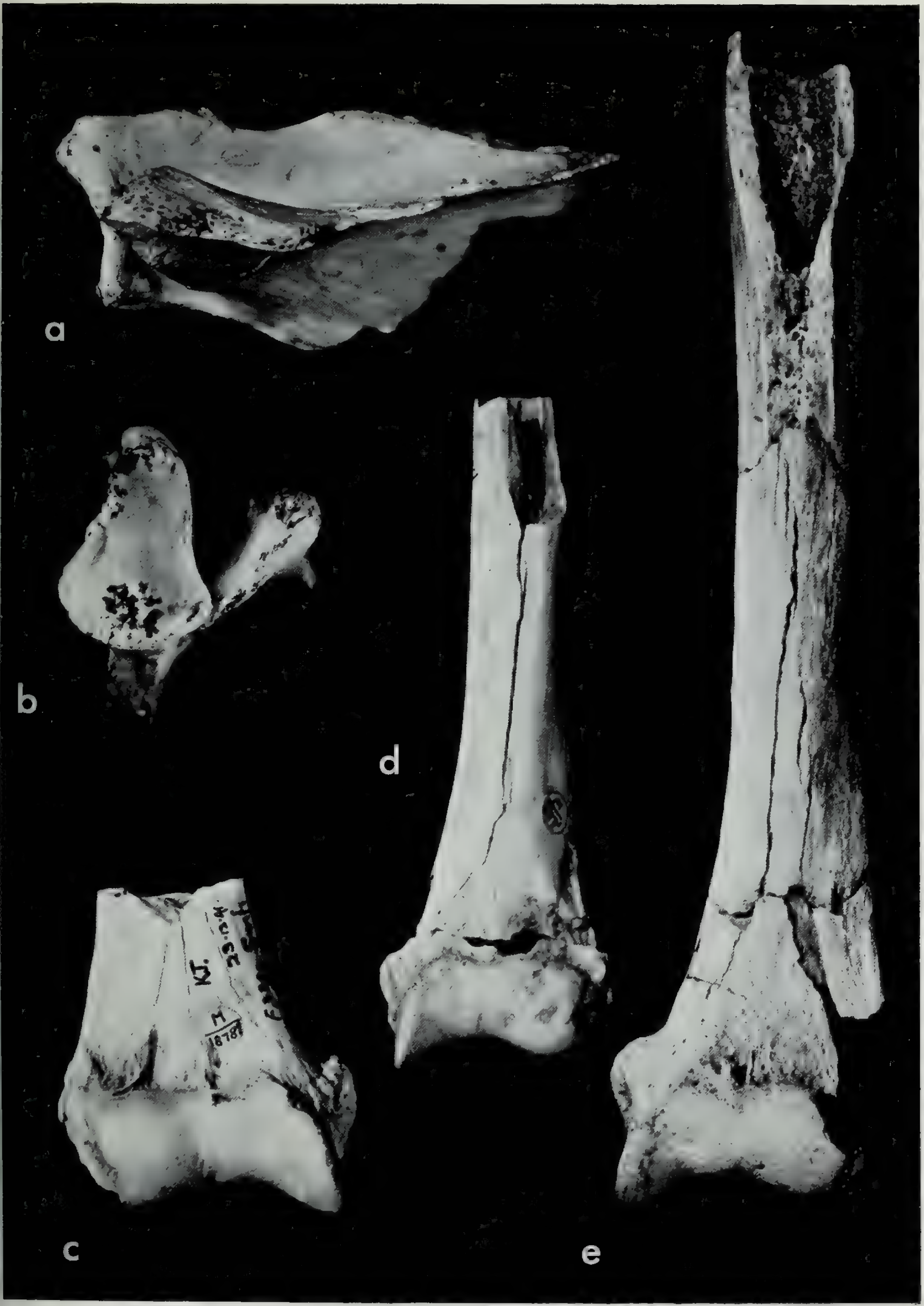

a
b
c
d
e

PLATE 12

Theropithecus oswaldi oswaldi

a-c. Ulnar fragments, radial aspect	
a. M 11546	× 3/4
b. M 18723	× 1
c. M 18726	× 1
d. M 18801 Radial fragment, probably male	× 1
e. M 11544 Radius, probably female	× 1

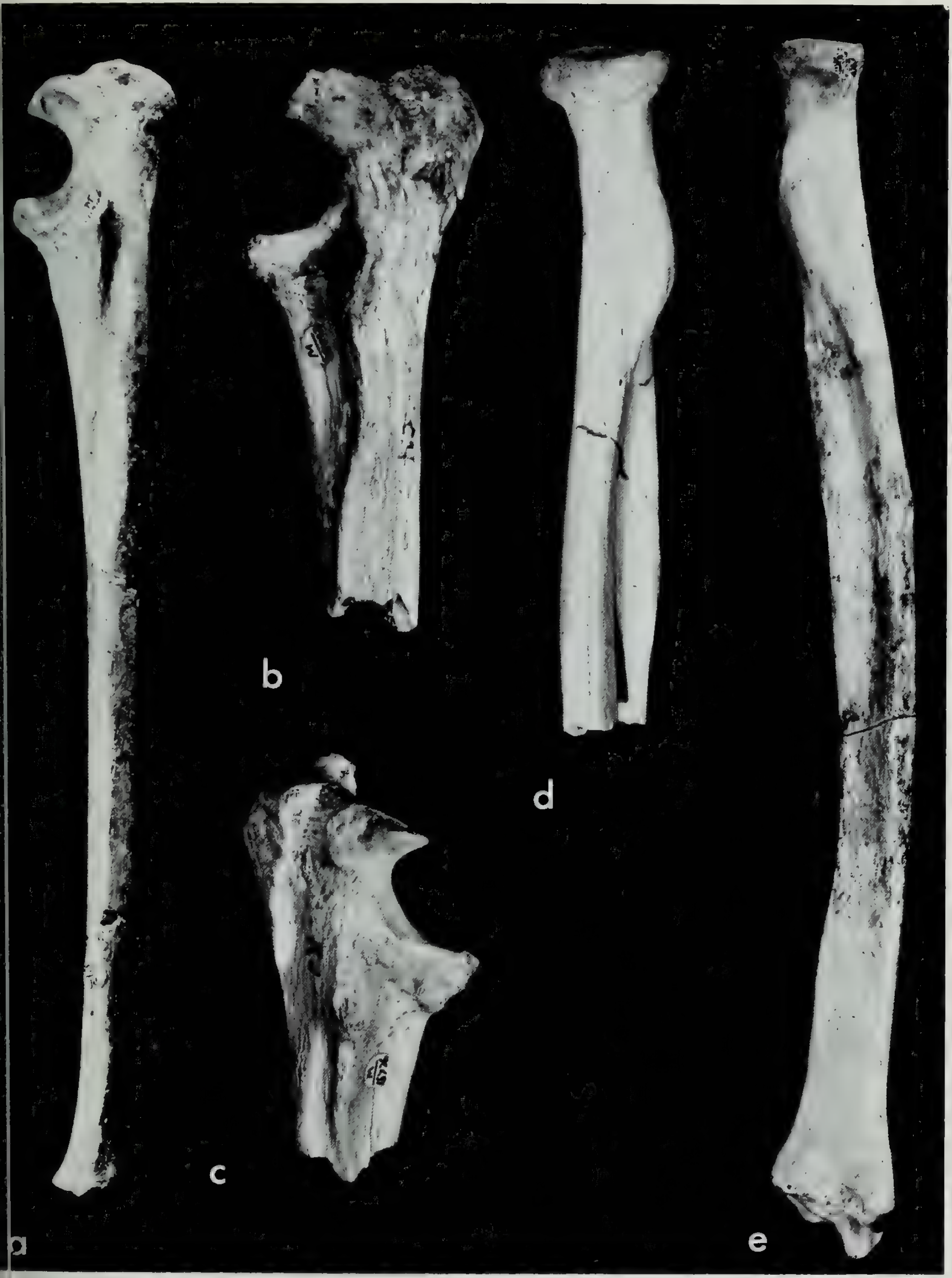

a
b
c
d
e

PLATE 13

Theropithecus oswaldi oswaldi

a. Femoral fragment, M 11548	× 1
b. Femoral fragment, M 18708	× 1
c. Femoral fragment, M 18707	× 1
d-f. Associated talus, M 11549, calcaneus, M 18806 and cuboid, M 18805	× 1

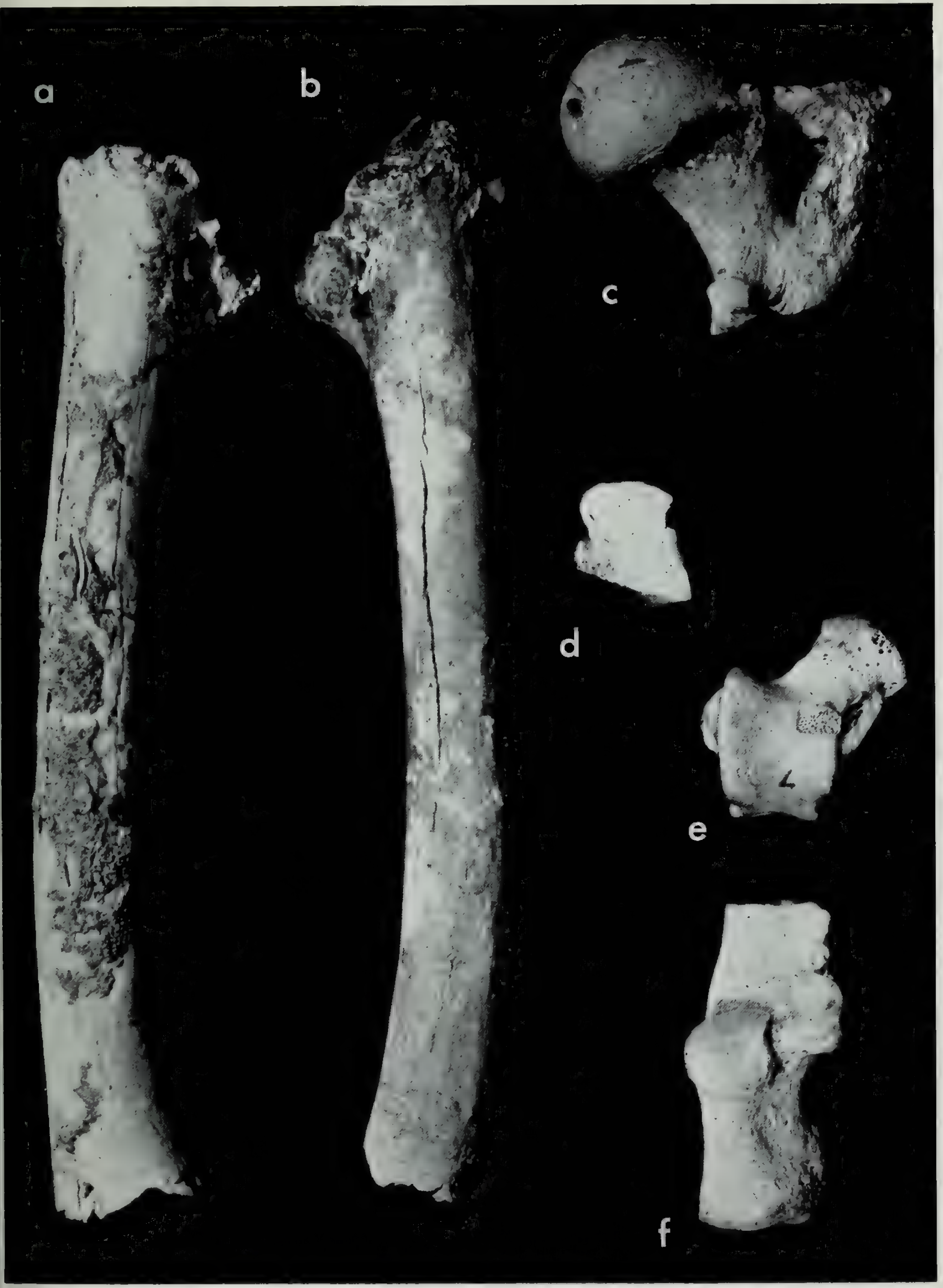

a
b
c
d
e
f

PLATE 14

Theropithecus oswaldi subsp.

a. Frontal fragment, M 18772	× 1
b, c. Maxillary fragment, M 14681	× 1
d, e. Maxillary fragment, M 18779	× 1

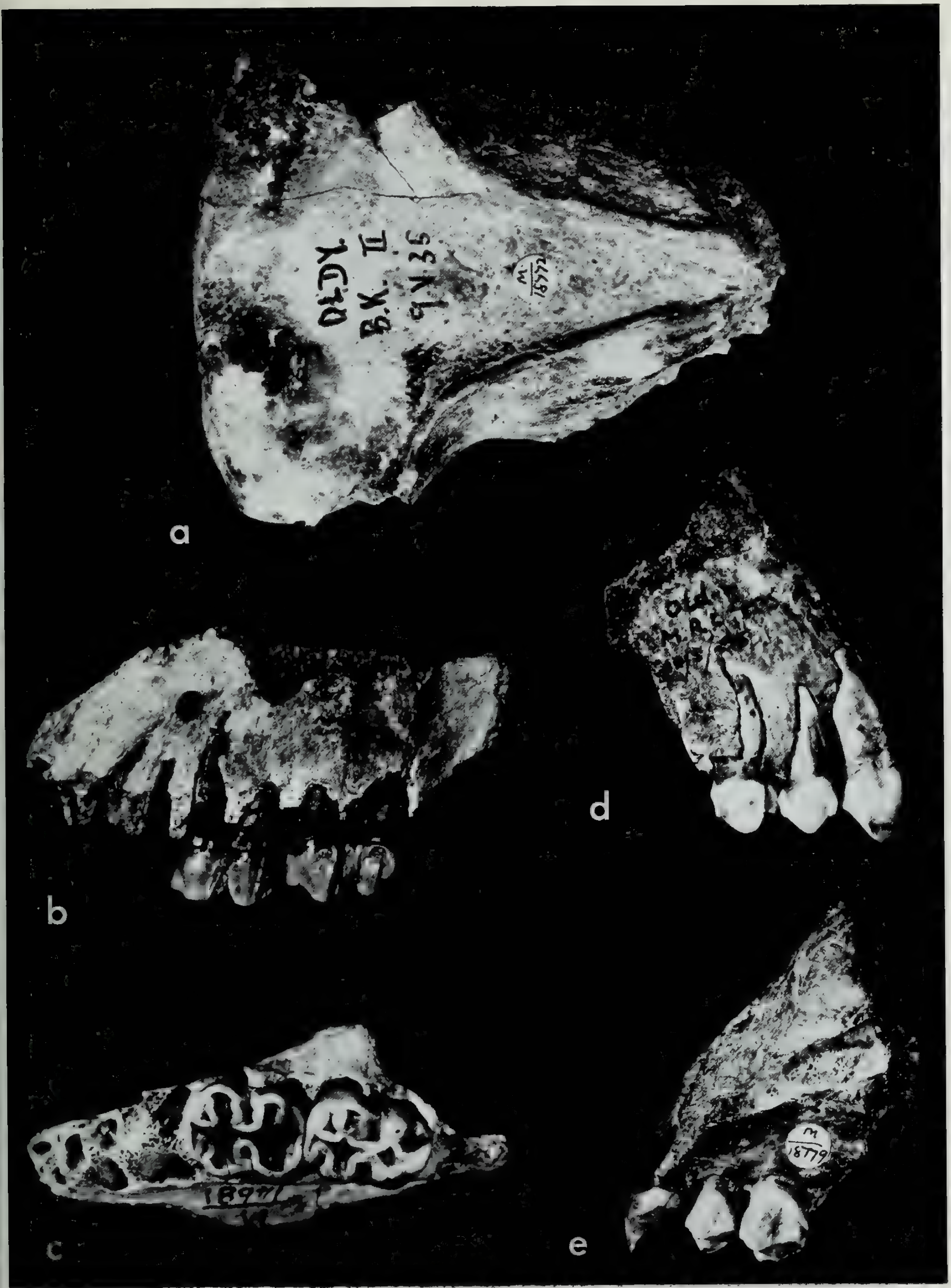

a
b
d
c
18971
e
M 18779

PLATE 15

Theropithecus oswaldi subsp., Olduvai

a,b.	Juvenile female mandibular fragment (c in list)	× 1
c,d.	Female mandibular fragment, M 14953	× 1

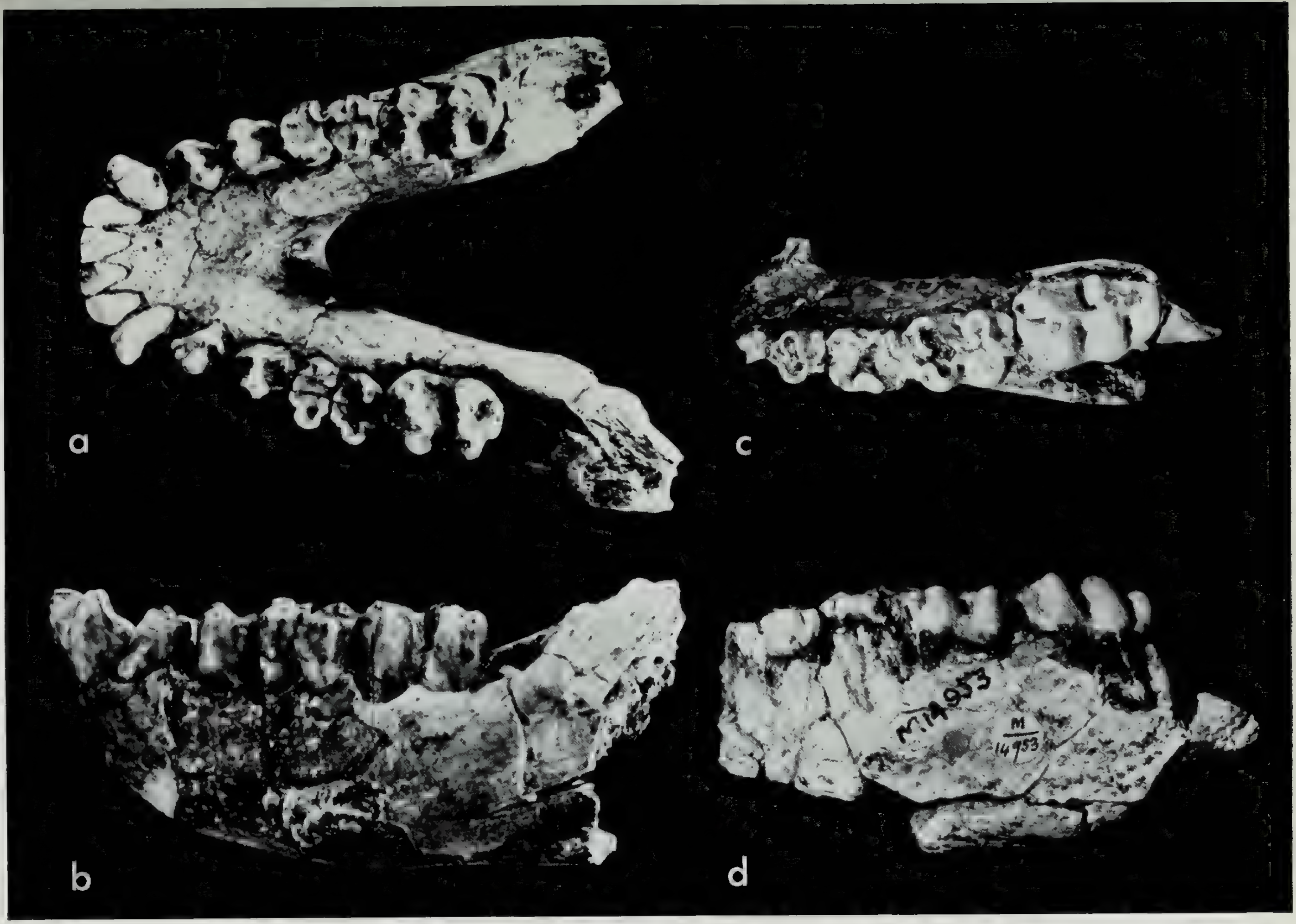

a
c
b
d
M14953
M
14953

PLATE 16

Theropithecus oswaldi leakeyi and ***Theropithecus darti,*** Olduvai

a, b. Juvenile male mandibular fragment (Type of *Simopithecus leakeyi*) M 14680 × 1

c, d. *Theropithecus darti* (Lower Bed II). Female mandibular fragment, M 14938 × 1

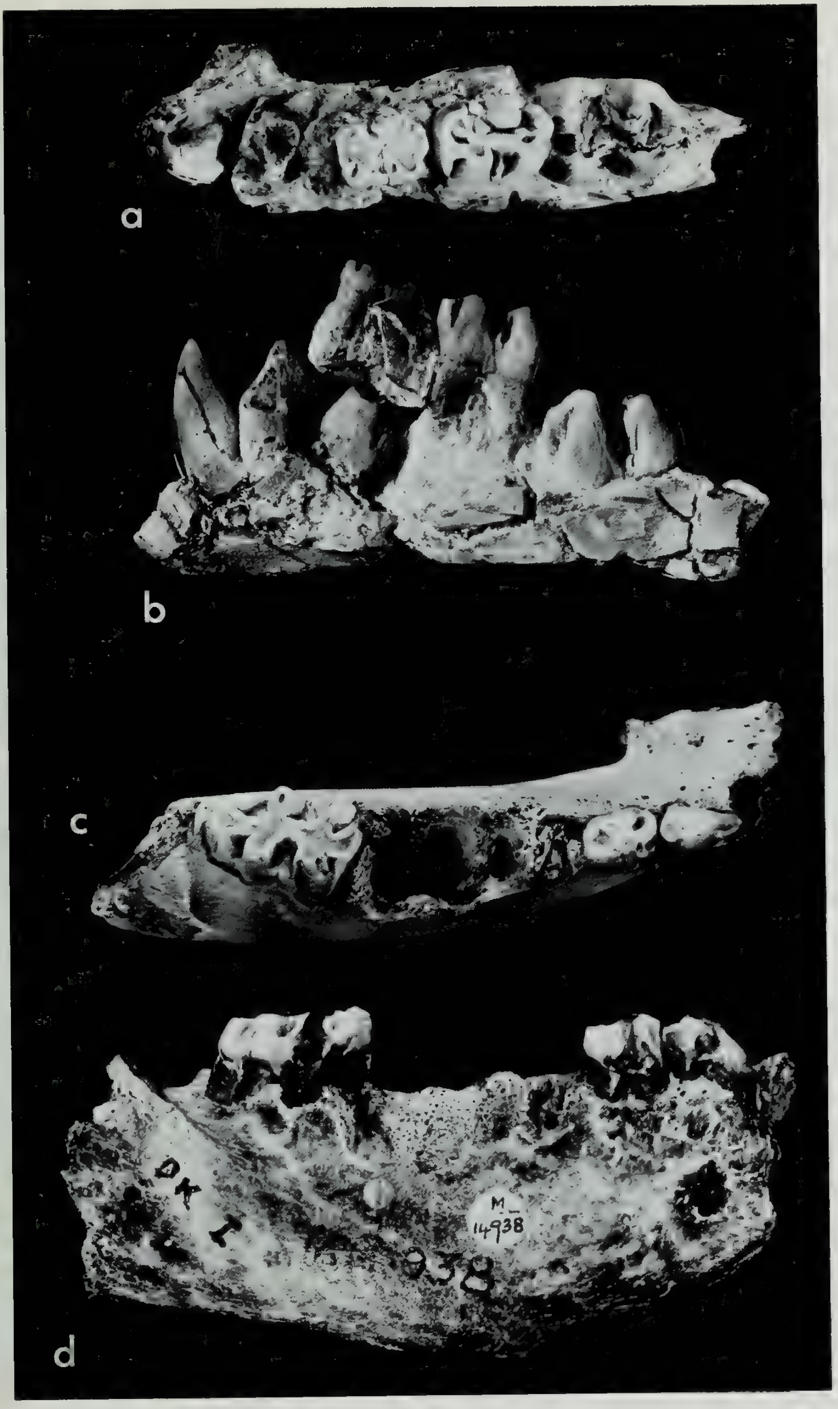

a
b
c
DK I
M
14938
d

PLATE 17

Theropithecus oswaldi subsp., Olduvai

a. Female calvarium (b in list)	× 2/3
b. Femoral fragment	× 2/3
c. Humeral fragment	× 2/3
d. Humeral fragment	× 2/3

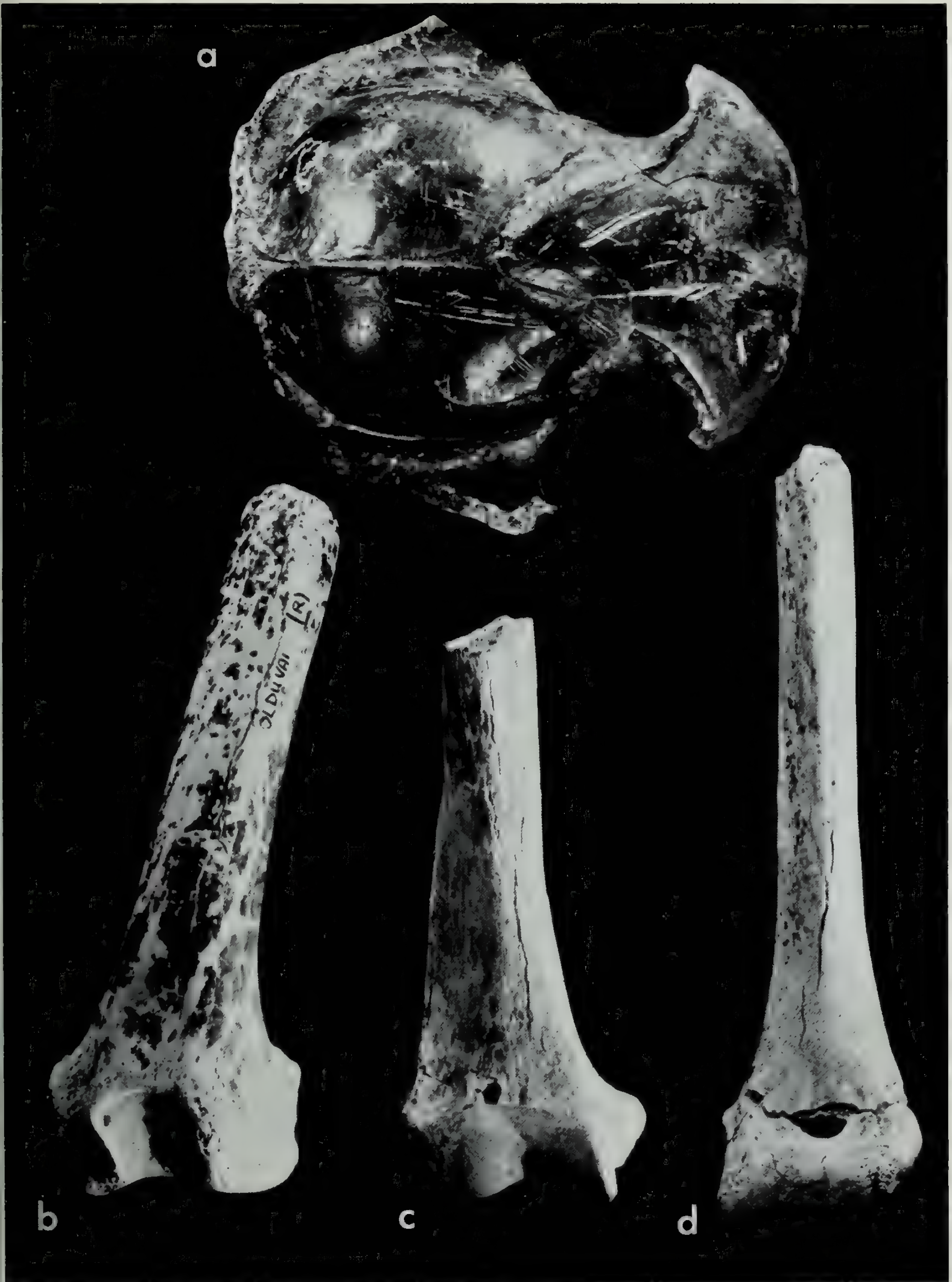

a
OLDUVAI
(R)
b
c
d

PLATE 18

Theropithecus oswaldi mariae**,** mandibular fragments

a. Female KNM-OG 0002 (Type)	× 1
b. Juvenile male KNM-OG	× 1
c. Juvenile male KNM-OG	× 1

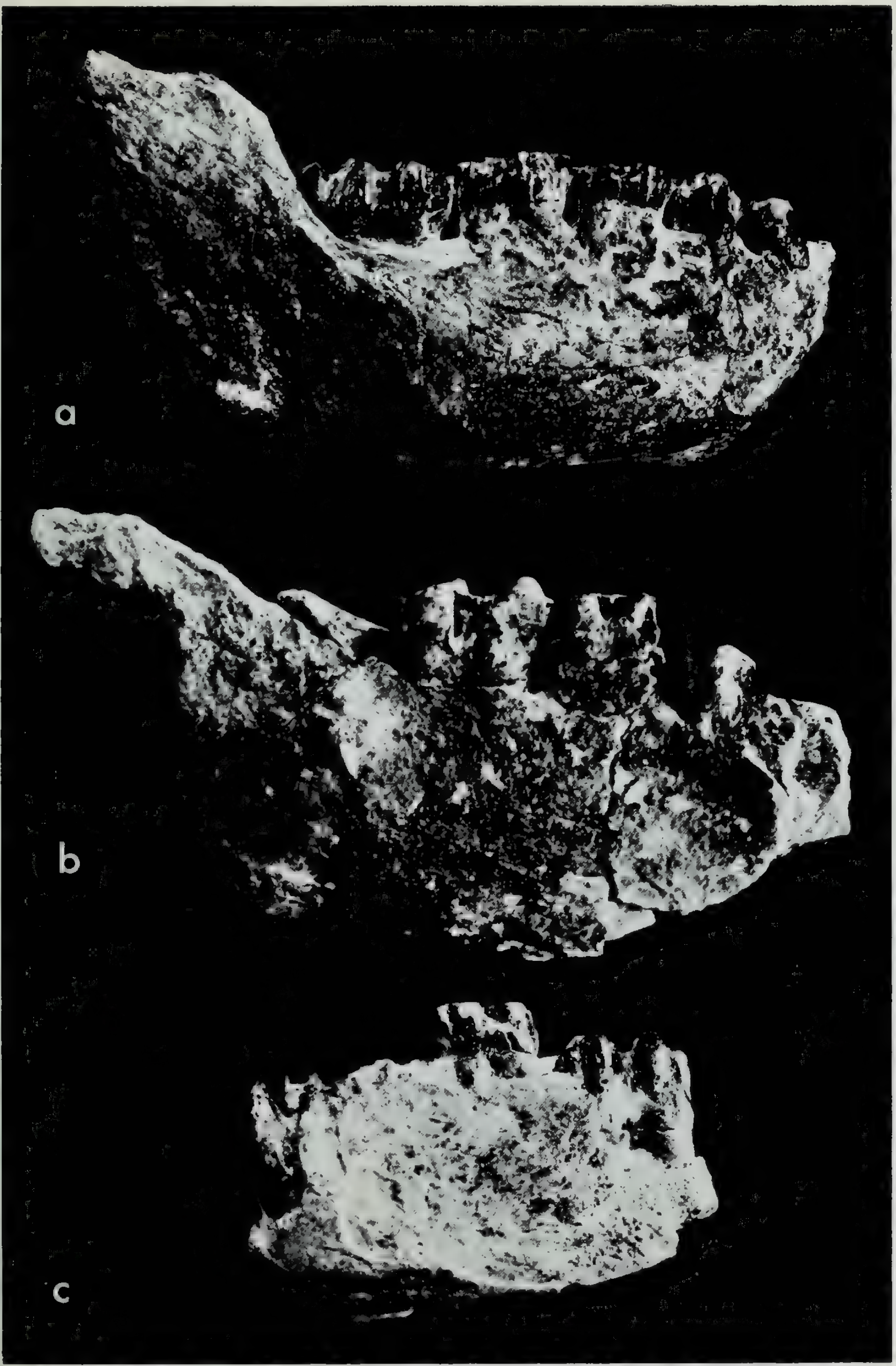

a
b
c

PLATE 19

Theropithecus oswaldi mariae

a,b. Adult male KNM OG-4	× 1
c. Adult male KNM OG-5	× 1
d. Juvenile maxillary fragment KNM OG-1	× 1

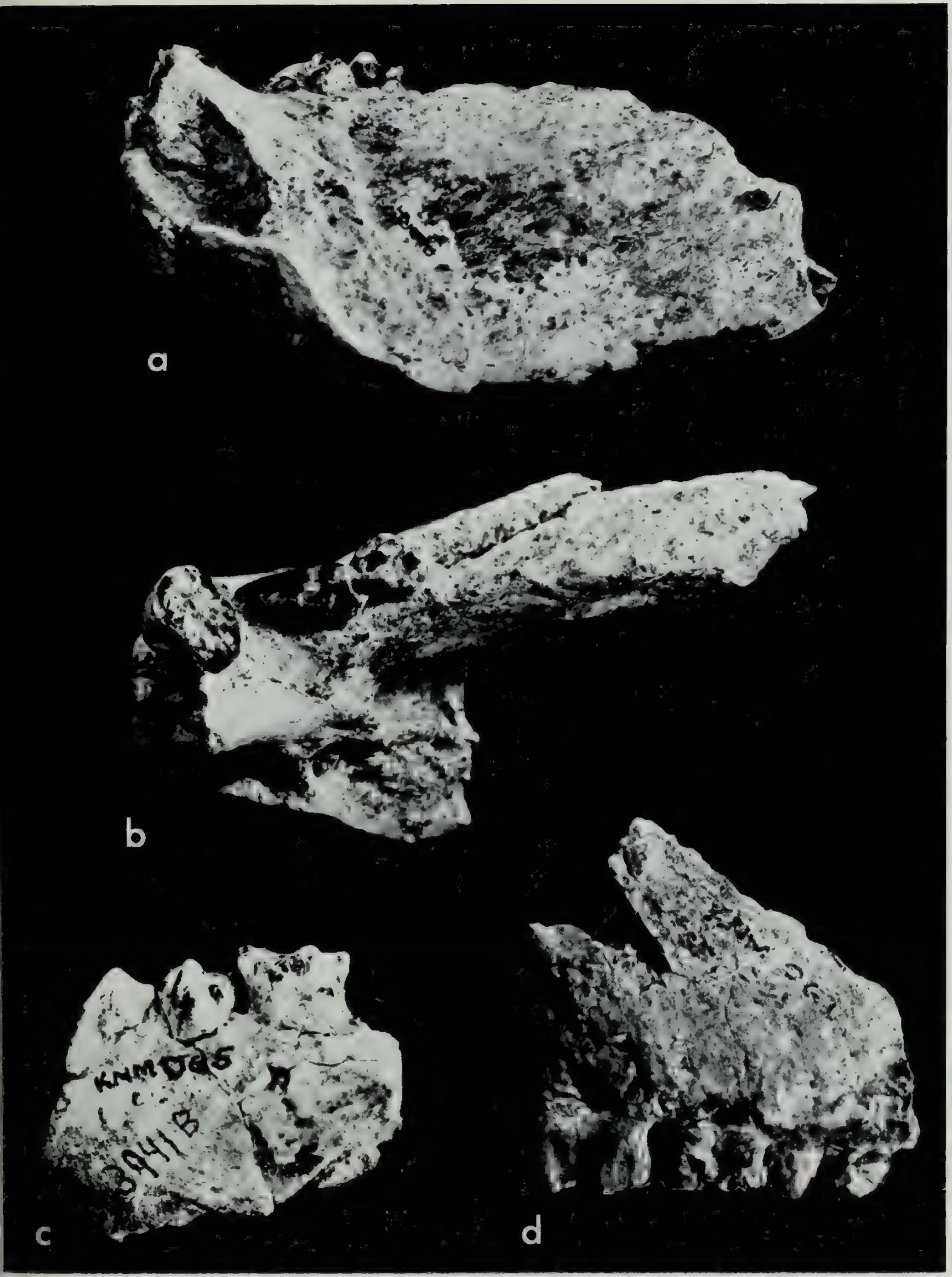
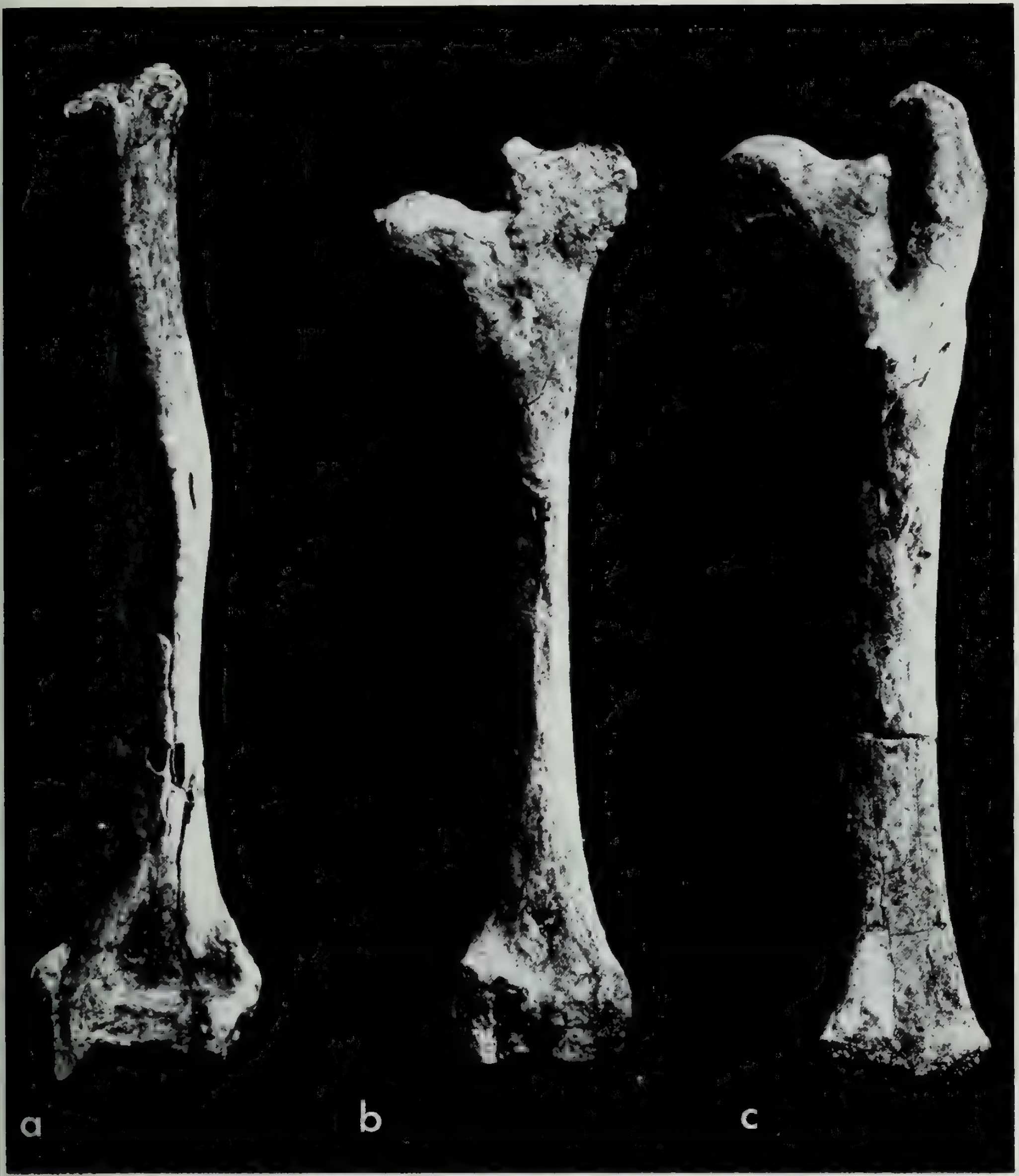

a
b
KNM DO5
C
3941 B
c
d

PLATE 20

Theropithecus oswaldi mariae

a. Humeral fragment, KNM-OG 1056. Probably subadult male	× ½
b. Femur, KNM-OG 10990. Probably female.	× ½
c. Femoral fragment, KNM-OG 1088. Probably male	× ½


a
b
c

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LLANDOVERY CONODONTS FROM THE WELSH BORDERLAND

R. J. ALDRIDGE

BULLETIN OF
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GEOLOGY Vol. 22 No. 2
LONDON : 1972

LLANDOVERY CONODONTS FROM THE WELSH BORDERLAND

- 5 JAN 1973
NATURAL HISTORY

BY
RICHARD JOHN ALDRIDGE
University of Nottingham, England

Pp. 125–231; 9 *Plates,* 13 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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LLANDOVERY CONODONTS FROM THE WELSH BORDERLAND

By R. J. ALDRIDGE

CONTENTS

		Page
I.	INTRODUCTION	128
II.	PREVIOUS RESEARCH ON LOWER SILURIAN CONODONTS	132
III.	TECHNIQUES	134
IV.	DETAILS OF SAMPLING LOCALITIES	135
	(a) Llansantffraid ym Mechain, Montgomeryshire	135
	(b) The Hope Valley, Shropshire	135
	(c) The Long Mynd Outcrop, Shropshire	138
	(d) Wenlock Edge, Shropshire	138
	(e) The Malvern Hills	141
	(f) Woolhope, Herefordshire	143
	(g) Tortworth, Gloucestershire	143
V.	THE CONODONT FAUNAS	143
	(a) General Review	143
	(b) Stratigraphic Distribution	143
	(c) Conodont Zones	151
	(i) The *Icriodella discreta—Icriodella deflecta* Assemblage Zone	151
	(ii) The *Hadrognathus staurognathoides* Assemblage Zone	151
	(iii) The *Icriodella inconstans* Assemblage Zone	153
	(iv) The *Pterospathodus amorphognathoides* Assemblage Zone	153
	(d) Correlation with Europe and North America	153
	(e) Faunal Provincialism	156
	(f) Facies Control	158
	(g) Homeomorphy	159
VI.	SYSTEMATIC PALAEONTOLOGY	160
VII.	CONCLUSIONS	220
VIII.	ACKNOWLEDGEMENTS	221
IX.	REFERENCES	222
X.	APPENDIX	226
	(a) List of sample localities	226
	(b) Sample weights and conodont abundances	227
	(c) Register of figured specimens	228

ABSTRACT

Conodont extraction techniques were applied to rock samples from Llandovery and early Wenlock strata of Wales and the Welsh Borderland. The samples yielded 11,750 identifiable specimens, referred to 36 genera and 108 species and subspecies. The species *Amorphognathus tenuis, Diadelognathus nicolli, Icriodella deflecta, Icriodella inconstans, Icriodella malvernensis, Ozarkodina alisonae, Spathognathodus abruptus* and *Spathognathodus gulletensis* are new.

The genera *Icriodella* and *Spathognathodus* are particularly valuable in local stratigraphy. The faunas are divided into four conodont assemblage zones, spanning an interval from the Idwian to the early Wenlock. These zones are compared with those recognized in Europe and North America.

The existence of two faunal provinces in the *Icriodina irregularis* Assemblage Zone, recognized in North America by Pollock, Rexroad & Nicoll (1970), is substantiated by the British faunas. The probable existence of three provinces in Telychian (C_5) times is also recognized. The local distribution of simple cones is significantly related to sea-depth, abundances being greatest in deeper water.

It is concluded that conodonts are of considerable value in Llandovery stratigraphy. Further research should establish phylogenetic lineages and enable precise definition of zones. Precise international correlations will only be achieved when the full effects of faunal provincialism and facies control are appreciated.

I. INTRODUCTION

THE distribution of outcrops of Llandovery strata in Wales and the Welsh Borderland is shown in Text-fig. 1. The Llandovery Series of the type area around Llandovery, Carmarthenshire, was mapped by O. T. Jones, who in 1925 published a detailed account of the southern part. Jones proposed a division of the Llandovery Series into three units, referred to as A (Lower Llandovery), B (Middle Llandovery) and C (Upper Llandovery). He further recognized lithological subdivisions of each unit, designated A_1 to A_4 for the Lower, B_1 to B_3 for the Middle and C_1 to C_6 for the Upper Llandovery. Cocks, Toghill & Ziegler (1970) defined four stage names, consistent with contemporary stratigraphic nomenclature, within the Llandovery Series. The stage names Rhuddanian, Idwian, Fronian and Telychian were proposed as alternatives or substitutes for the letters and numbers used by Jones. The relationship between the two schemes is illustrated in Text-fig. 2.

A succession of graptolite assemblage zones was established in the British Lower Palaeozoic graptolitic sequences by Lapworth (1879–80) and Elles & Wood (1901–18). This scheme, with some subsequent modification, has become accepted as a standard for international correlation. Eleven graptolite zones span the Llandovery (Text-fig. 2), the base being taken at the base of the *Glyptograptus persculptus* Zone and the top at the base of the *Cyrtograptus centrifugus* Zone. Direct reference of the almost exclusively shelly sequence at Llandovery to these zones has only been achieved at three horizons, where Jones (1925 : 360, 370; 1949 : 52) recorded diagnostic graptolites (Text-fig. 2). The association of C_5 brachiopods with *greistoniensis* Zone graptolites in the Welsh Borderland was recorded by Cocks and Walton (1968 : 226) and by R. K. Jones *et al.* (1969), thus providing an additional, indirect tie between the type succession and the graptolitic sequences.

Brachiopods are currently used for the correlation of outcrops of the shelly facies. Evolutionary lineages for the genera *Eocoelia* and *Stricklandia*/*Costistricklandia* were tabulated by Ziegler, Cocks & McKerrow (1968 : text-fig. 2) and are reproduced in Text-fig. 3. In addition, brachiopods have proved to be valuable indicators of sea-depth, particularly in the Fronian and Telychian. Five animal communities, each named after a prominent brachiopod genus, have been recognized in collections dominated by brachiopods (Ziegler 1965; Cocks 1967; Ziegler, Cocks & Bambach 1968). These are, in order of increasing depth, the *Lingula* community, the *Eocoelia* community, the *Pentamerus* community, the *Stricklandia* community and the *Clorinda* community. *Eocoelia* may be replaced by a homeomorph rhynchonellid possibly referable to the genus *Rostricellula* (Cocks & Rickards 1969 : 220, 222). In C_5 and C_6, *Pentamerus* is replaced by *Pentameroides* and *Stricklandia* by *Costistricklandia*.

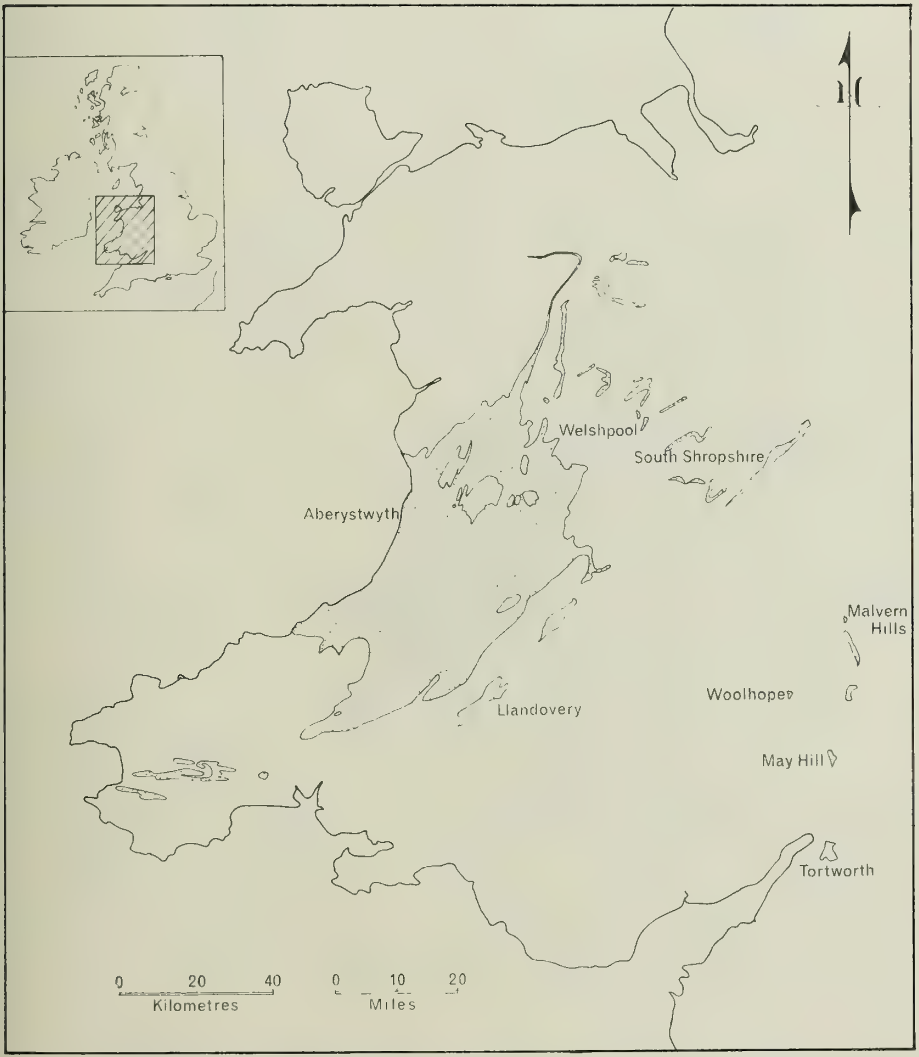
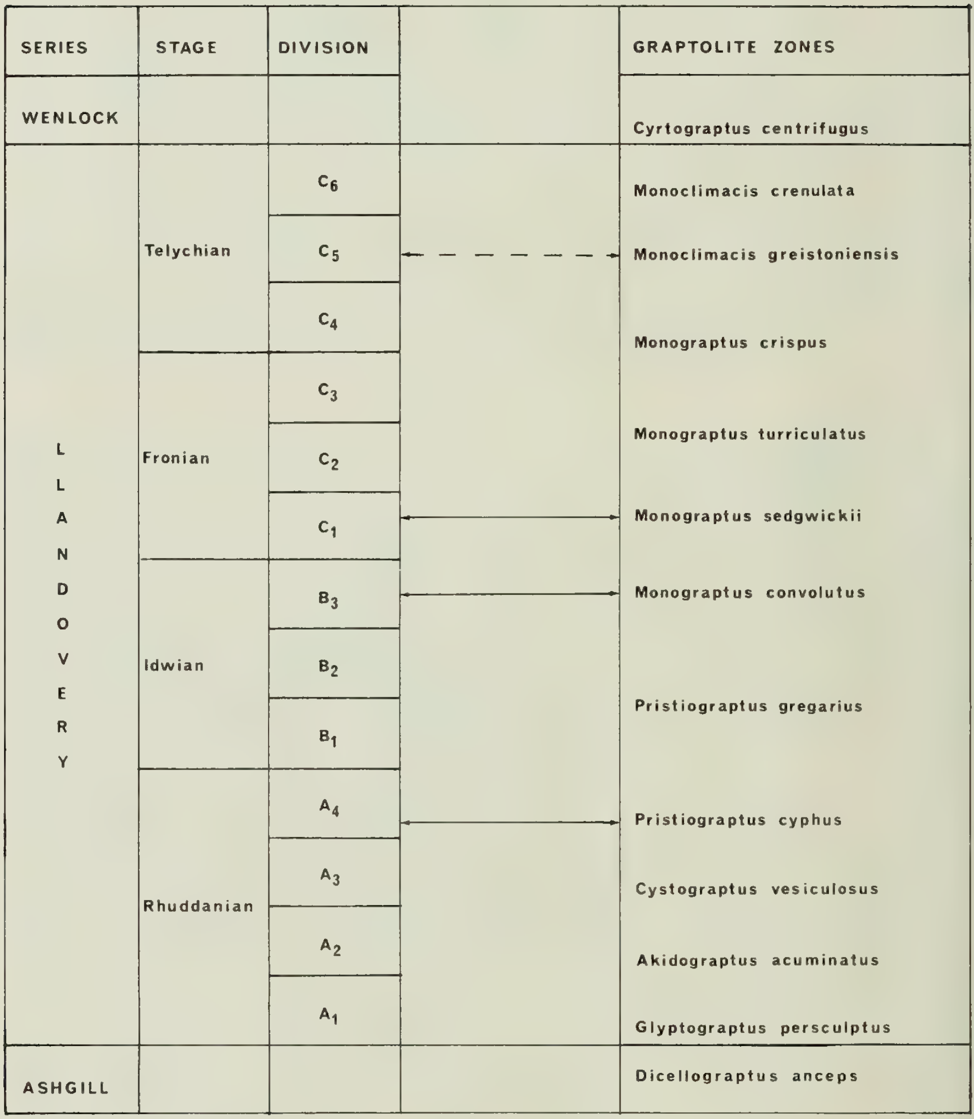

Welshpool
South Shropshire
Aberystwyth
Malvern Hills
Woolhope
Llandovery
May Hill
Tortworth
0 20 40
Kilometres
0 10 20
Miles

FIG. 1. Outcrop pattern of the Llandovery Series in Wales and the Welsh Borderland.



SERIES	STAGE	DIVISION		GRAPTOLITE ZONES
WENLOCK				Cyrtograptus centrifugus
LLANDOVERY	Telychian	C_6		Monoclimacis crenulata
		C_5	← — — — — — →	Monoclimacis greistoniensis
		C_4		Monograptus crispus
	Fronian	C_3		
		C_2		Monograptus turriculatus
		C_1	←——————→	Monograptus sedgwickii
	Idwian	B_3	←——————→	Monograptus convolutus
		B_2		
		B_1		Pristiograptus gregarius
	Rhuddanian	A_4	←——————→	Pristiograptus cyphus
		A_3		Cystograptus vesiculosus
		A_2		Akidograptus acuminatus
		A_1		Glyptograptus persculptus
ASHGILL				Dicellograptus anceps

←——————→ Direct ties at Llandovery

← — — — — — → Indirect ties outside the type area

FIG. 2. Llandovery Stages (Cocks, Toghill & Ziegler 1970), Lithological Divisions (Jones 1925) and Graptolite Zones.

WENLOCK					
LLANDOVERY	Telychian	C6	Eocoelia sulcata	Costistricklandia lirata typica	Pentameroides
		C5	Eocoelia curtisi	Costistricklandia lirata alpha	
		C4	Eocoelia intermedia	Stricklandia lens ultima	Pentamerus
	Fronian	C3			
		C2	Eocoelia hemisphaerica	Stricklandia lens progressa	
		C1			
	Idwian	B3		Stricklandia lens intermedia	
		B2			
		B1			
	Rhuddanian	A4		Stricklandia lens typica	
		A3			
		A2		Stricklandia lens prima	
		A1			
ASHGILL					

FIG. 3. Llandovery brachiopod lineages and their relationship to the stages and lithological divisions defined in the type area (after Ziegler, Cocks & McKerrow 1968).

The value of conodonts as an additional tool for stratigraphic correlation, both locally and internationally, is examined in this paper. The stratigraphic distribution of conodonts in the Llandovery and early Wenlock of Wales and the Welsh Borderland has been investigated by means of samples collected from a number of well-documented localities. The British faunas are compared with those described from the European continent by Walliser (1964) and from North America by Rexroad (1967), Nicoll & Rexroad (1968) and Pollock, Rexroad & Nicoll (1970). The effects of faunal provincialism on geographic distribution are examined in the light of existing evidence. Comparisons are made between the distribution of conodonts and brachiopods in the shelly facies of the Llandovery in an attempt to recognize some of the effects of facies control on local geographic distribution.

II. PREVIOUS RESEARCH ON LOWER SILURIAN CONODONTS

The first systematic description of a lower Silurian conodont fauna was published by Branson & Branson (1947), who described seventeen species from the Brassfield Formation of Kentucky. They considered the species *Icriodina irregularis* to have the most stratigraphic value, as it was readily identifiable, stratigraphically restricted and abundant.

The next major contribution was made by Walliser (1957, 1962, 1964), who published detailed accounts of Silurian and lower Devonian conodonts from Europe. Walliser (1964) proposed a provisional division of the Silurian into eleven conodont zones, three of which (Bereich I, the *celloni*-Zone and the *amorphognathoides*-Zone) are represented in Llandovery strata. The type section for these zones is within a condensed sequence exposed at Cellon in the Carnic Alps of Austria (Walliser 1964 : pl. 1). The conodont fauna of Bereich I displays similarities to upper Ordovician faunas, with the genera *Ambalodus* and *Amorphognathus* present throughout. The upper part of Bereich I is characterized by specimens referred by Walliser to *Icriodina irregularis*. The *celloni*-Zone is characterized by abundant specimens of *Neospathognathodus celloni* and *Ozarkodina adiutricis*; the *amorphognathoides*-Zone is characterized by *Pterospathodus amorphognathoides* and *Ozarkodina gaertneri*.

After the publication of Walliser's work Llandovery conodont faunas were reported from many parts of the world. Manzoni (1965) recognized Bereich I and the *amorphognathoides*-Zone in the central and eastern Carnic Alps and Schönlaub (1969) recorded Llandovery conodonts from the Hohe Trieb region of the Carnic Alps. Spasov (1966) recorded *N. celloni*, *P. amorphognathoides* and other lower Silurian species in the Balkan peninsula and Spasov and Filipović (1966) recognized the *amorphognathoides*-Zone in Bosnia. Stein (1964 : fig. 17; 1965 : fig. 5) recorded conodonts in the Llandovery of the Frankenwald, Bavaria. Drygant & Tsegelnyuk (1968) found *amorphognathoides*-Zone conodonts in association with *Monoclimacis* cf. *crenulata* in the Retevsky horizon of the Silurian of Podolia. The *celloni*-Zone and the *amorphognathoides*-Zone were recognized in several sections in the northern greywacke belt of the Kitzbuhl Alps, Tyrol, Austria by Mostler (1966, 1967, 1968) and Al-Hasani & Mostler (1969).

Fragmentary Llandovery conodonts have been recorded from Thailand in black shales containing *Monograptus cyphus* (Igo & Koike 1966 : 15). Igo & Koike (1967, 1968) also recorded a lower Silurian conodont fauna containing *N. celloni* and *P. amorphognathoides* within the Setul Limestone sequence of the Langkawi Islands, Malaya.

In North America, Rexroad (1964) reported the occurrence of *Icriodina* in the lower Silurian of Kentucky and noted the presence of two younger conodont zones. Rexroad recognized the close resemblance between North American and European lower Silurian conodont faunas and pointed out their potential use in international correlation. In 1965 Rexroad & Rickard published the results of their attempt to recognize Walliser's Silurian zones in the Niagara Gorge section of North America. Several zones, including the *amorphognathoides*-Zone, were identified. The *celloni*-Zone was not recognized in the Gorge, but *N. celloni, O. adiutricis* and other characteristic species were recovered from the Reynales Limestone in New York. Rexroad & Rickard (1965 : 1218, text-fig. 1) suggested that the boundary between the *celloni*-Zone and the *amorphognathoides*-Zone coincided with the boundary between the Llandovery and the Wenlock.

Rexroad (1967) next described the conodont fauna of the Brassfield Formation in the Cincinnati Arch region of Kentucky and Ohio. The dominant important species was *Icriodina irregularis*, with *Icriodina stenolophata* and *Spathognathodus oldhamensis* also being characteristic. Rexroad referred the fauna to the upper part of Walliser's Bereich I. This correlation was based largely on the presence of *Icriodina*, although Rexroad (1967 : 34) considered that specimens referred to this genus by Walliser were in fact fragments of *Icriodella* (at that time regarded by Rexroad to be a junior synonym of *Scyphiodus*). The position of the boundary between Bereich I and the *celloni*-Zone was to some extent clarified by Rexroad's report in this paper (1967 : 13) of the recovery by Bergström of high Bereich I or low *celloni*-Zone conodonts in association with graptolites referable to the *Monograptus sedgwickii* Zone.

Nicoll & Rexroad (1968) extended the limits of the Brassfield Formation to include the Lee Creek Member at the top, and described the conodont faunas of this new member and of the overlying Salamonie Dolomite in Indiana and Kentucky. The overlap of *N. celloni* at the lower end of its range with *I. irregularis* and at the upper end with *P. amorphognathoides* was regarded by Nicoll & Rexroad as an indication that slight redefinition of Walliser's zonal scheme was necessary. They therefore proposed the erection of three assemblage zones, the *Icriodina irregularis* Assemblage Zone, the *Neospathognathodus celloni* Assemblage Zone and the *Pterospathodus amorphognathoides—Spathognathodus ranuliformis* Assemblage Zone. The critical point of Nicoll & Rexroad's zonal scheme was their definition of the *Neospathognathodus celloni* Assemblage Zone by the total range of the genus *Neospathognathodus*. Walliser (1964 : table 1) showed that *Neospathognathodus pennatus*, which occurs as a complementary form to *P. amorphognathoides*, ranged throughout the *amorphognathoides*-Zone in Europe. As pointed out by Schönlaub (*in* Jaeger & Schönlaub 1970), this necessitates the conclusion that the whole of the *celloni*- and *amorphognathoides*-Zones of Europe are equivalent to the *Neospathognathodus celloni* Assemblage Zone of North America. This clearly is not what Nicoll

& Rexroad believed nor what they intended in their definition, as they stated (1968 : 7) that their *N. celloni* Zone included the larger part, if not all, of Walliser's *celloni*-Zone and the lower part of his *amorphognathoides*-Zone. It follows that the boundary between the *N. celloni* Zone and the *P. amorphognathoides—S. ranuliformis* Zone of North America is, at present, unsatisfactorily defined. Craig (1969) applied both the European and North American zonal schemes to the sequence of lower Silurian conodont faunas he investigated from the Batesville district of Arkansas.

Conodonts from the *Icriodina irregularis* Assemblage Zone and from older Silurian strata of northern Michigan and Ontario were described by Pollock, Rexroad & Nicoll (1970). The fauna of the *I. irregularis* zone differed appreciably from that of time-equivalent strata in the Cincinnati Arch area and the authors considered that this was due to faunal provincialism. In particular, *Icriodina* itself was absent and was replaced by *Icriodella* as the dominant platform element. Pollock *et al.* proposed the erection of the *Panderodus simplex* Assemblage Zone for those faunas below the *I. irregularis* zone and above characteristic Ordovician faunas.

There are few records of Llandovery conodonts from Britain. Whittard (1927 : 743) noted their presence in the Pentamerus Beds of Harper's Dingle, Shropshire, and Squirrel & Tucker (1960 : 178) listed conodont genera from the upper Haugh Wood Formation of the Woolhope Inlier, Herefordshire. Brooks & Druce (1965) described forty specimens, referable to nine species, from a limestone conglomerate at the base of the Wych Formation at Gullet Quarry in the Malvern Hills. On the basis of six specimens of a spathognathodid, which they identified as *Spathognathodus* cf. *celloni*, they referred the fauna to the *celloni*-Zone. The conodonts from an upper Llandovery limestone exposed at Hollybush Quarry in the Malvern Hills were listed by Jones, Brooks, Bassett, Austin & Aldridge (1969), who also re-examined the Wych Formation in Gullet Quarry. The Hollybush Quarry fauna included specimens of *Neospathognathodus celloni*, but these were not considered to be conspecific with the specimens described by Brooks & Druce. Species characteristic of both the *celloni*-Zone and the *amorphognathoides*-Zone were abundant in the Hollybush and in the Gullet collections.

III. TECHNIQUES

Techniques of conodont extraction have become well-established and the most efficient method of large-scale recovery has proved to be the disintegration of calcareous rocks by dilute acetic, monochloracetic or formic acid. This method has an additional advantage in the commonly high quality of preservation of conodonts in limestones. Calcareous rocks were, therefore, collected preferentially in the field. The shale and turbidite sequences of west-central Wales lack calcareous strata, but thin limestone horizons are comparatively common in the shelf successions of the Welsh Borderland and adjacent parts of Wales. Calcareous rocks are rare in the type area around Llandovery. The hard mudstones and arenites of the Llandovery area resisted all attempts at disintegration, and the rare calcareous horizons did not yield conodonts. The stratigraphic distribution of Llandovery conodonts was, therefore, examined in the Welsh Borderland by means of collections from several separate localities. This approach necessitated concentration on major exposures, for which adequate stratigraphic information was already available.

The standard laboratory techniques of digestion in 10% acetic acid and separation of the residues in bromoform were employed to recover conodonts from calcareous rock samples. Selected specimens were coated with ammonium chloride or magnesium oxide prior to photography. Photographs were taken using a Leitz Dialux polarizing microscope and a Leica M3 35 mm camera loaded with Kodak Panatomic X film.

IV. DETAILS OF SAMPLING LOCALITIES

Each of O. T. Jones' subdivisions of the Llandovery Series, with the exception of the uppermost (C_6), was sampled at a well-documented locality within the type area. No identifiable conodonts were recovered from any of the samples, nor from samples collected at the Sawdde Gorge, Llandeilo (SN/715260) and the Craig-wen Quarry, Meifod (SJ/099091) in Wales; Middletown (SJ/301128), Buttington Brick Works (SJ/265100), the Norbury to Linley Lane (SO/359928), the Onny River section (SO/426853) and Gilberries Brook (SO/512926) in Shropshire. Conodonts recovered from the Rhuddanian Powis Castle Formation of the Gwern-y-Brain section (SJ/219128), near Welshpool, Montgomeryshire, were most probably derived from locally exposed Upper Ordovician strata.

Samples that yielded conodonts were collected from several localities, viz.:

a. Llansantffraid ym Mechain, Montgomeryshire

Conodonts, including the species *Icriodella discreta* and *Icriodina irregularis* were recovered from limestone bands exposed in a trackside quarry 200 m north-west of Gelli Farm (SJ/236193) (Text-fig. 4). The age of these beds in terms of the type succession has not been established, but Whittington (1938 : 440) equated them with the V_{2b} subdivision defined at Meifod, Montgomeryshire by King (1928). Ziegler, Cocks and McKerrow (1968 : 768) gave a range from late Rhuddanian possibly into the Fronian for the V_2 Formation. The Gelli Farm Quarry sequence, therefore, is probably of Idwian age.

b. The Hope Valley, Shropshire

The outcrop pattern of the Llandovery Series in South Shropshire is shown in Text-fig. 5. Two Llandovery formations, the Venusbank Formation and the Minsterley Formation, were defined in the Hope Valley area of the outcrop bordering the Shelve by Ziegler, Cocks & McKerrow (1968 : 742). The type section for both formations is in Hope Brook.

The Venusbank Formation is exposed in Hope Quarry (SJ/355021), where 10 m of thickly-bedded sandstones, becoming flaggy towards the top, are displayed. The basal calcareous sandstone is not exposed in the quarry face, but was collected from a small roadside exposure in front of the quarry. This sample (H.Q.1) and sample H.Q.3, from low in the section, yielded abundant conodonts, including *Icriodella deflecta*, *Icriodina irregularis*, *Spathognathodus abruptus*, *S. hassi* and *S. oldhamensis*.

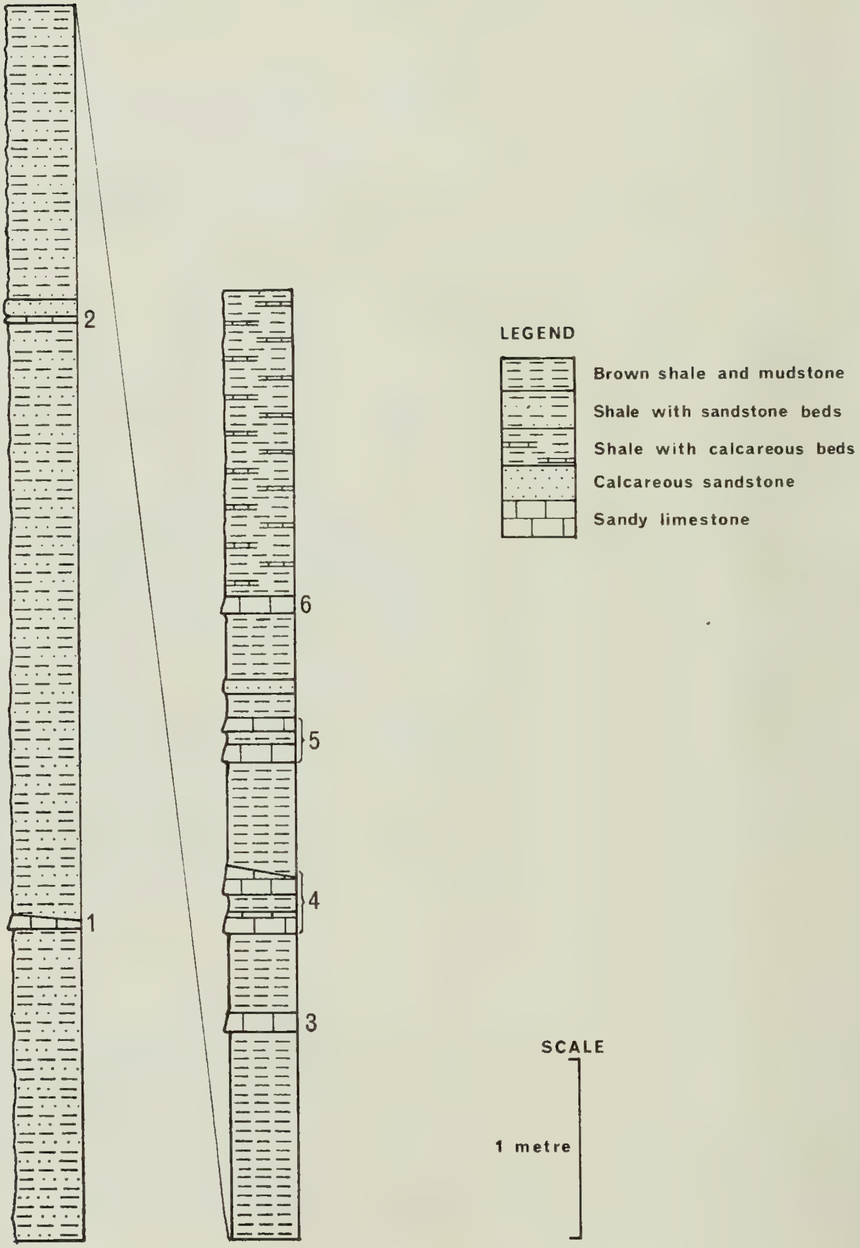

2
1
6
5
4
3
LEGEND
Brown shale and mudstone
Shale with sandstone beds
Shale with calcareous beds
Calcareous sandstone
Sandy limestone
SCALE
1 metre

FIG. 4. Section at Gelli Farm Quarry, Llansantffraid ym Mechain. The base and top of the formation are not exposed. The horizons of samples Gelli Farm 1–6 are indicated.

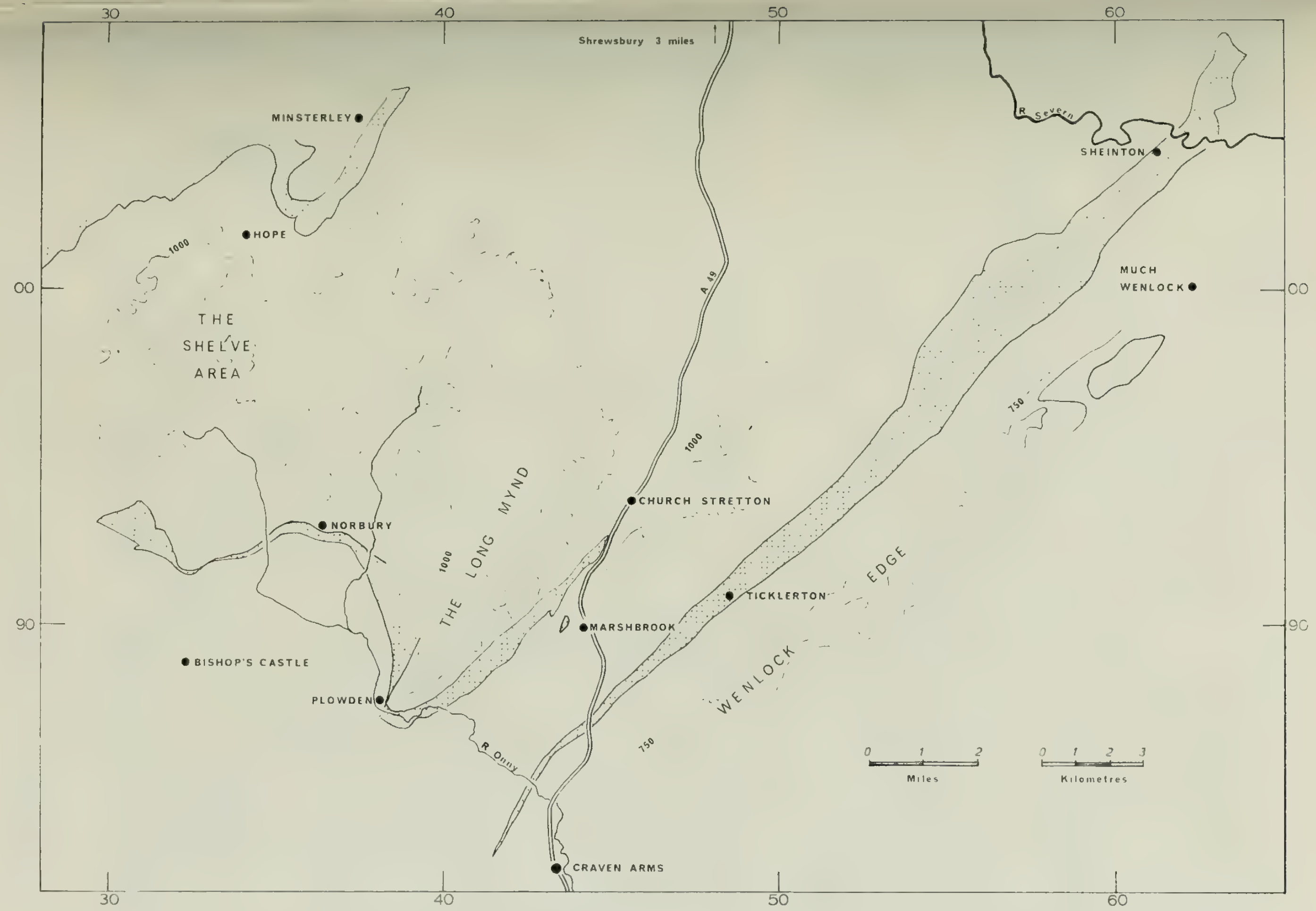

30
40
50
60
00
90
Shrewsbury 3 miles
MINSTERLEY
HOPE
1000
THE SHELVE AREA
NORBURY
BISHOP'S CASTLE
PLOWDEN
THE LONG MYND
1000
A 49
1000
CHURCH STRETTON
MARSHBROOK
R Onny
750
CRAVEN ARMS
TICKLERTON
WENLOCK EDGE
750
R Severn
SHEINTON
MUCH WENLOCK
0 1 2
Miles
0 1 2 3
Kilometres

FIG. 5. Outcrops of the Llandovery Series in South Shropshire. After Whittard (1928, 1932) with minor modifications.

Small numbers of conodonts were also recovered from samples taken higher in the section. An Idwian age for the lower part of the Venusbank Formation is indicated by the presence of *Climacograptus* sp. and *C.* aff. *rectangularis* (Ziegler, Cocks & McKerrow, 1968 : 744).

The Minsterley Formation comprises some 130 m of mudstones with thin arenaceous and calcareous beds. The only evidence of age is in Whittard's (1932 : 877) record of the presence at one horizon of *Monograptus halli* and *M. becki*, which Cocks & Rickards (1969 : 225) referred to the *turriculatus* Zone. Calcareous levels within the Minsterley Formation were collected in Hope Brook (Text-fig. 6, samples H.V.3–6, H.B.1, 2) and in the lane from Minsterley to Habberley (SJ/380049). The lowest part of the formation contained *Ambalodus anapetus*, *Aphelognathus siluricus* and *Spathognathodus abruptus*. Higher in the sequence there are few significant forms, but *Hadrognathus staurognathoides* first appears in sample H.V.4. *Spathognathodus* n. sp. A is characteristic of the Minsterley Lane collections. The highest conodont-bearing horizon found in the Minsterley Formation was a limestone conglomerate, sample H.B.2, which contained *Icriodella inconstans*, *Spathognathodus gulletensis* and *S. ranuliformis*. In the Malvern Hills, these species are characteristic of C_5 strata.

c. The Long Mynd outcrop, Shropshire

In the Marshbrook outlier, at the eastern end of the Long Mynd outcrop, the Llandovery Pentamerus Beds are soft, dark mudstones with arenaceous and calcareous bands. Abundant conodonts were recovered from samples collected at a small stream exposure 250 m south-west of New House Farm (SO/434898). Direct evidence of the age of these beds is lacking, but the Pentamerus Beds of the nearby Hamperley Borehole contained graptolites of *convolutus* and *sedgwickii* Zone age (Cocks & Rickards 1969 : 217). Cocks (personal communication, 1970) suggested that a reasonable age for the New House, Marshbrook exposure is within B_1–C_1 and probably in the B_{2-3} region. Important conodont species recovered included *Ambalodus anapetus*, *Aphelognathus siluricus*, *Amorphognathus tenuis*, *Icriodella deflecta*, *Icriodina irregularis*, *Spathognathodus abruptus*, *S. hassi* and *S. oldhamensis*. A similar conodont fauna was collected from a characteristic section in the limestones and shales of the Pentamerus Beds displayed in a road cutting west of Hillend Farm, Plowden (SO/396877). The section sampled is depicted in Text-fig. 7, where the horizons of samples Plowden 1–8 are indicated. *Eocoelia hemisphaerica* has been recovered from these beds, indicating a C_{1-2} age (Ziegler, Cocks & McKerrow 1968 : 746).

The Pentamerus Beds are also extensively exposed around the village of Norbury, where sandstone is the dominant lithology. Samples from an exposure in the roadside south of the church (SO/364928) yielded conodonts, *Hadrognathus staurognathoides* being the most significant form. Brachiopods have not been recorded from this locality, but exposures to the west of the village contain *Eocoelia intermedia*, indicative of a C_{3-4} age (Ziegler, Cocks & McKerrow 1968 : 746).

d. Wenlock Edge, Shropshire

Several samples were obtained from the Pentamerus Beds of the Llandovery

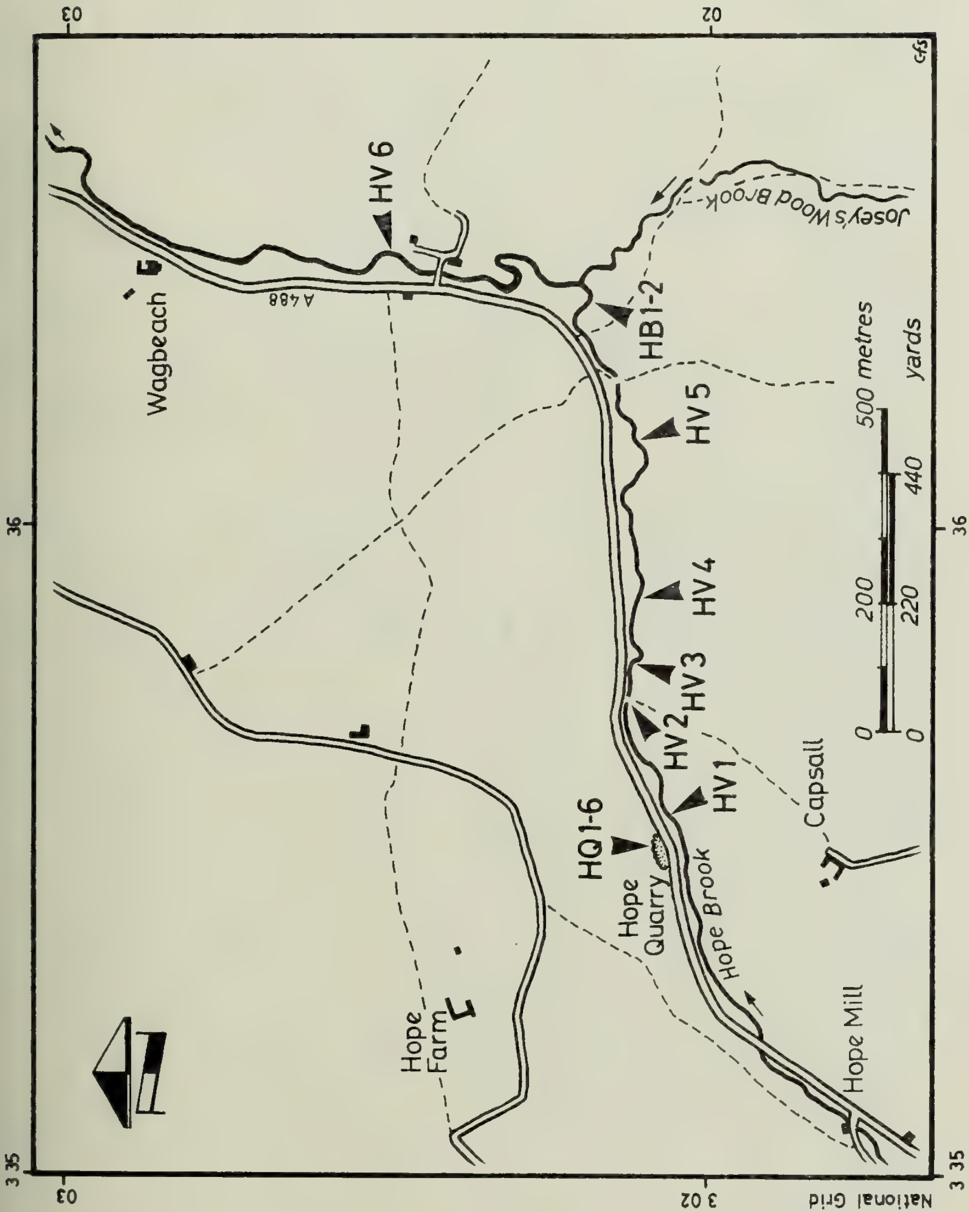

Wagbeach
A488
HV6
HB1-2
Josey's Wood Brook
HV5
HV4
HV3
HV2
HV1
HQ1-6
Hope Quarry
Hope Brook
Capsall
Hope Mill
Hope Farm
500 metres
yards
0
200
0
220
440
03
02
36
3 35
3 02
National Grid
cfs

FIG. 6. Sample localities in the Hope Valley.

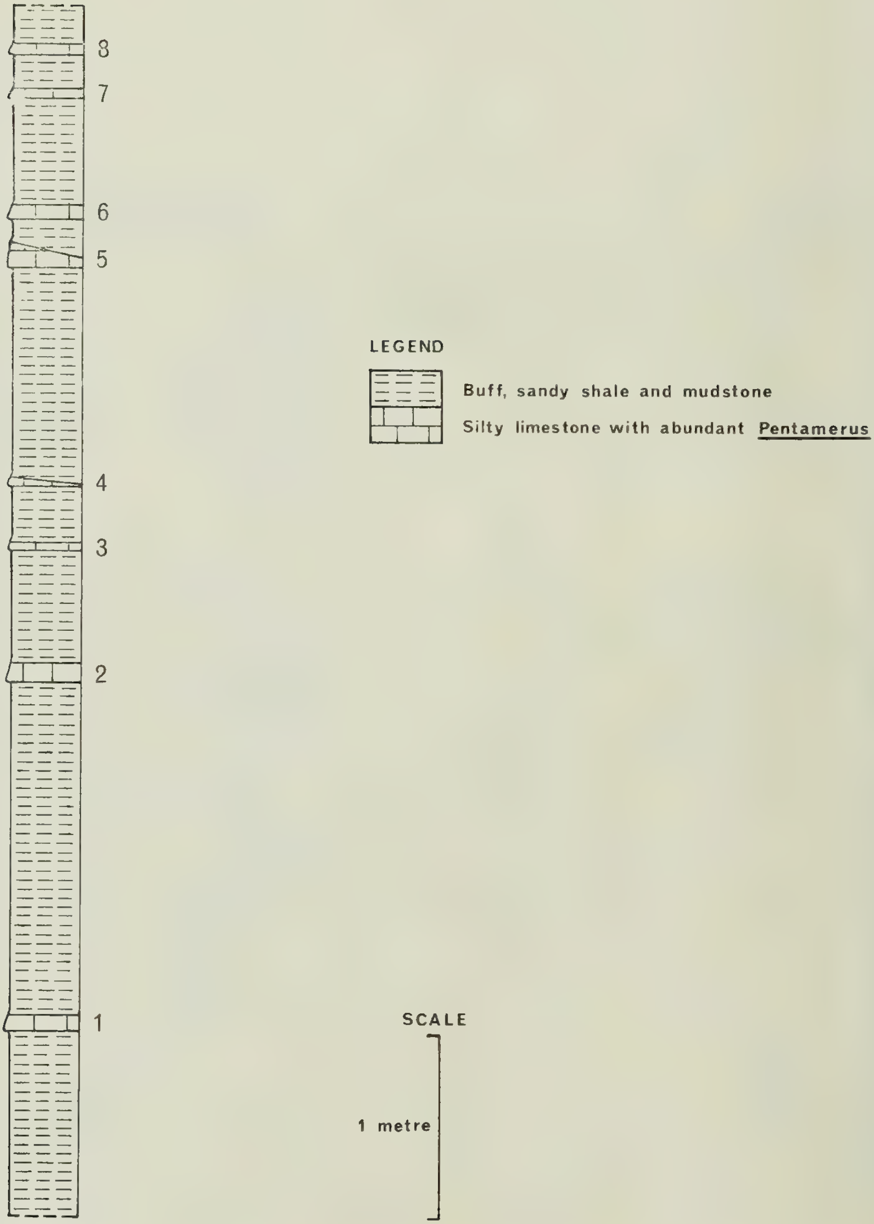

8
7
6
5
4
3
2
1
LEGEND
Buff, sandy shale and mudstone
Silty limestone with abundant Pentamerus
SCALE
1 metre

FIG. 7. Section in the Pentamerus Beds at Hillend Farm, Plowden. The base and top of the formation are not exposed. The horizons of samples Plowden 1–8 are indicated.

outcrop lying parallel to Wenlock Edge, but only one, from Ticklerton Brook (SO/482909), yielded a significant number of conodonts. Ziegler, Cocks & McKerrow (1968 : 748) recorded a C_{1-2} age for the strata at this locality. The only important conodont species recovered was *Spathognathodus oldhamensis*.

The Pentamerus Beds are conformably succeeded by the Hughley Shales. Beds at the base of this formation are exposed in Sheinton Brook, where a band of silty limestone is present in the sequence (SJ/612031). Ziegler, Cocks & McKerrow (1968 : 749) reported a C_{3-4} age for the limestone, which yielded abundant, well-preserved conodonts, including *Hadrognathus staurognathoides*, *Icriodella* cf. *I. malvernensis*, *Spathognathodus gulletensis*, *S. hassi* and *S.* n. sp. B. Samples collected from higher in the Hughley Shale did not yield conodonts.

A conodont fauna consisting of *Pterospathodus amorphognathoides* and characteristic associated forms was recovered from limestone bands near the base of the Wenlock Shale, exposed in a small stream south of Ticklerton (SO/481901).

e. The Malvern Hills

The Telychian Wych Formation of the Malvern Hills is displayed in a series of exposures to the west of the Pre-Cambrian massif. The well-known exposure in Gullet Quarry (SO/761318) displays the unconformable junction between the Wych Formation and the Pre-Cambrian. Above the unconformity about 30 m of sandstones, siltstones, shales and limestones are exposed (Text-fig. 8). The lower beds yielded *Eocoelia curtisi* and the higher beds *Costistricklandia lirata alpha*, indicative of a C_5 age (Ziegler, Cocks & McKerrow 1968 : 757). The basal bed is a limestone conglomerate, described in 1965 by Brooks & Druce, who supplied a sample from which conodonts have been extracted. Conodonts were abundant in samples (Gullet 1–3) from limestones in the main exposed sequence and included *Icriodella inconstans*, *Spathognathodus gulletensis* and *S. ranuliformis*. The same species were present in sample Gullet 4, from an isolated limestone lens above the main sequence. In addition, this sample contained *Apsidognathus tuberculatus*, *Neospathognathodus bullatus*, *N. celloni*, *N. pennatus* and many other important species.

The conodonts from a Telychian limestone in Hollybush Quarry (SO/760371) were listed by Jones, Brooks, Basset, Austin & Aldridge (1969 : 465), and are described herein. The presence of *Eocoelia curtisi* in the limestone indicates a C_5 age and graptolites referable to the *greistoniensis* Zone have also been recovered. *Icriodella inconstans*, *Spathognathodus gulletensis* and *Neospathognathodus celloni* were included in the conodont fauna. The conglomeratic base of the Wych Formation exposed at 'Sycamore tree Quarry', West Malvern (SO/765459), contained *Icriodella malvernensis* and other important species.

The conformable junction between the Wych Formation and the overlying Woolhope Limestone is exposed in Birches Farm Lane, near an open air school (SO/760468). Ziegler, Cocks & McKerrow (1968 : 757) found that the greater part of the Wych Formation is of C_6 age, and the beds of this exposure are presumably of high C_6 age. The conodont fauna recovered from a limestone band 1·5 m below the junction (sample Cowleigh Park 1) consisted of *Pterospathodus amorphognathoides*

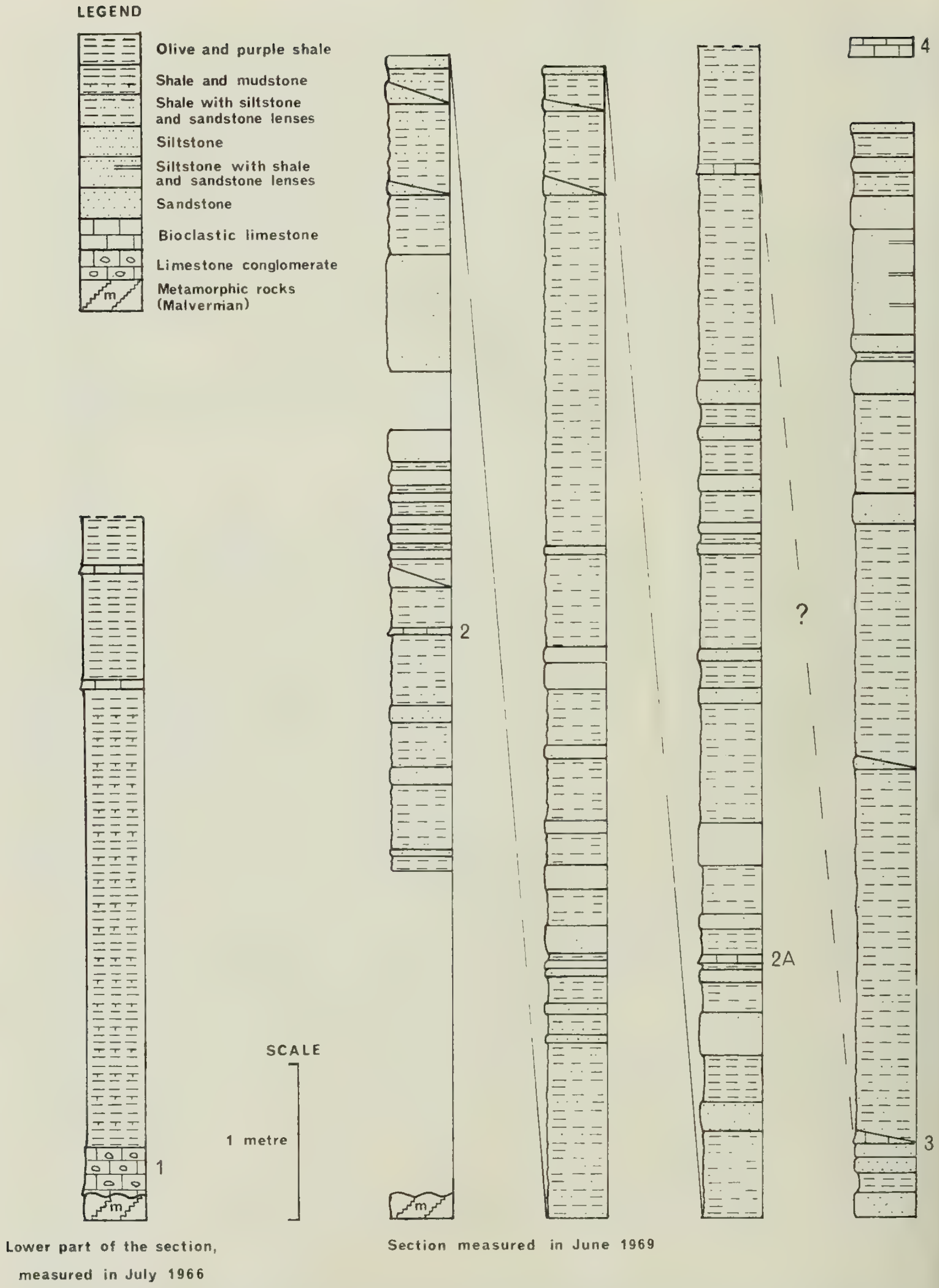

LEGEND
Olive and purple shale
Shale and mudstone
Shale with siltstone and sandstone lenses
Siltstone
Siltstone with shale and sandstone lenses
Sandstone
Bioclastic limestone
Limestone conglomerate
Metamorphic rocks (Malvernian)
m
1
2
2A
3
4
?
SCALE
1 metre
Lower part of the section, measured in July 1966
Section measured in June 1969

FIG. 8. Section in the Wych Formation at Gullet Quarry, Malvern Hills. The base of the formation is unconformable on the Malvernian. The upper part of the section is obscured by rubble and the top of the formation is not exposed. The horizons of samples Gullet 1–4 are indicated.

and characteristic associated forms. Samples from the Woolhope Limestone at this locality did not yield useful conodonts.

f. Woolhope, Herefordshire

A conodont fauna recovered from limestones at the top of the upper Haugh Wood Formation (sample Haugh Wood 3) at the track junction in Haugh Wood (SO/589358) included *Pterospathodus amorphognathoides* and *Ozarkodina gaertneri*. A C_6 age for this horizon is indicated by the presence of *Costistricklandia lirata typica* (Ziegler, Cocks & McKerrow 1968 : 757). The Woolhope Limestone south of Woolhope village (SO/612353) yielded abundant simple cones.

g. Tortworth, Gloucestershire

Collections made by the author from the Telychian strata of the Tortworth inlier did not yield a significant number of conodonts, but conodonts have been recovered from the Damery Formation near Damery Bridge (ST/706943) by Miss M. Roberts, who kindly made her collection available for description. *Icriodella inconstans* and *Spathognathodus gulletensis* were among the species present. Ziegler, Cocks & McKerrow (1968 : 761) recorded *Eocoelia curtisi* and *Costistricklandia lirata alpha* from the Damery Formation, indicative of C_5 age.

In addition, rock specimens collected by Dr A. M. Ziegler from localities listed in Ziegler, Cocks & McKerrow (1968) were kindly supplied by Dr W. S. McKerrow. Specimens M-G-C, from the C_5 Yartleton Beds of May Hill, and T-R-A, from the Damery Beds of Tortworth, yielded a small number of conodonts.

V. THE CONODONT FAUNAS

a. General Review

Of the 101 rock samples collected from Llandovery and early Wenlock strata of Wales and the Welsh Borderland, 58 yielded identifiable conodonts. A total of 11,750 specimens are referred to 36 genera and 108 species and subspecies. 34 of the genera and 94 of the species and subspecies are named. The species *Amorphognathus tenuis*, *Diadelognathus nicolli*, *Icriodella deflecta*, *Icriodella inconstans*, *Icriodella malvernensis*, *Ozarkodina alisonae*, *Spathognathodus abruptus* and *Spathognathodus gulletensis* are new. The collections are dominated by the genus *Panderodus*, to which about half the specimens are referred. *Panderodus unicostatus* is by far the most abundant species and is represented by 3,750 specimens.

b. Stratigraphic Distribution

No idnigenous conodonts were recovered from strata of Rhuddanian age. The distribution of conodonts recovered from strata of Idwian, Fronian, Telychian and early Wenlock age is summarised in Tables 1–4. The genera of most stratigraphic value are the platforms and *Spathognathodus*. Some species of the bar and blade genera are also useful, but the simple cones appear to be of very limited stratigraphic value.

TABLE I

Conodont Stratigraphic Ranges: I

SAMPLE NO / SPECIES	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6			
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Ticklerton 1–3
Acodus curvatus					21	4	6	35		2		4	10							2
A. unicostatus	6		1		35	6	26	83	3	5	2	2	9	1			2			4
Ambalodus anapetus		100		19		13														
A. galerus													44							
Ambalodus spp.	2	2		2	4			1												
Amorphognathus tenuis		47		13																
Aphelognathus siluricus		7		19		4														
Apsidognathus tuberculatus													60							
Astrognathus tetractis													16							
Astropentagnathus irregularis														1						
Aulacognathus kuehni												14		3						
Carniodus carinthiacus																	73	7		25
C. carnicus																	13			2
C. carnulus													2				81	1		48
C. carnus													2	1			68	2		26
Carniodus spp.		15		3																
Diadelognathus nicolli																				11
D. primus									1											
Distacodus obliquicostatus							1													
Distomodus? egregius				10						15		5	4	1	1		6			4
D? extrorsus		3	6	4					5		5	4		7	1			1		
D. kentuckyensis	2	6	10	27		2	1	3	10	13	9	14	7	6		1	2	2		7
D. triangularis tenuirameus					3								10							
D. triangularis triangularis		17		6								4	17				27			17
Distomodus n. sp.										3										
Distomodus? spp.			1	5						2		2	2			1				
Drepanodus aduncus										1				1			12	1		2
D. suberectus		7	8		2	5						3	14	1	1					
Drepanodus spp.	1		2	1	8			1					4							2
Exochognathus brassfieldensis	4	2	6	14	1	2		2	2	4	1		14	1	4					1
E. brevialatus		23	4	3		1	1					1								13

TABLE II

Conodont Stratigraphic Ranges: II

SAMPLE NO. / SPECIES	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6			
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Tickleton 1–3
Exochognathus caudatus		3		6						13	2	7	12	2	2		7			8
E. detortus			3	3						8		4		1			10	1		6
E. keislognathoides		6	10	1		1	1													
E. latialatus																	25	3		
Exochognathus n. sp.				1																
Exochognathus spp.	3	13	5	14		1	1	1	4	3	6	3	1	2	2	1	1	1		5
Gothodus? n. sp.		3					1													
Hadrognathus staurognathoides								1	3	16	2	26	1	3	3	1	5	4		5
Hibbardella? prima				2																
H? trichonodelloides										5			2				2			
Hibbardella n. sp.										3										
Hindeodella equidentata				13	6	6		20	1	1		4	8	3	2		2			4
Hindeodella spp.		[illegible]	3	15		1	2	21			2	2	4	1				1	2	2
Icriodella deflecta		13	38	2																
I. discreta	15																			
I. inconstans											6	186	121	13	3	27				
I. malvernensis															63					
I. cf. I. malvernensis										2										
Icriodina irregularis	1	1	2	8																
Icriodina sp.								1												
Ligonodina kentuckyensis		1	6	10	5	11	1	6	1	15	5	1	1							11
L. petila										1			3							6
L. salopia		3				1				1		2					2			7
L. silurica				4			2		1	11		13	3	1						
L? variabilis				4		1		4	1	23		21		1						12
Ligonodina spp.		3	4	9	1	4	1	1	4		6	5	7		5					17
Lonchodina detorta				1		1		17	1	6	1									
L. fluegeli								17		4										
L. greilingi	1		4	5	7	2		7		5		4	1				2			3
L. walliseri		1	4	9	1	11	1	1	3	11	4	4	4		2	1	2			25
Lonchodina sp. A			1	1				2				1								

TABLE III

Conodont Stratigraphic Ranges: III

SAMPLE NO / SPECIES	LLANDOVERY																		lower Wenlock	
	B_{1-3}			C_{1-2}					C_{3-4}		C_5						C_6			
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Tickleton Brook	H. V. 3	Minsterley Lane	H. V. 4	Norbury 1–3	Sheinton 2	H. B. 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Tickleton 1–3
Lonchodina sp. B				4	1	3	1			3			2							
Lonchodina sp. C										1										23
Lonchodina spp.				2				4				1								1
Neoprioniodus costatus costatus														1			34	4		37
N. costatus paucidentatus			2	1								2	21							
N. excavatus	1	3	3	5	1	1		5	3	4	1	3	13	1			1	1		14
N. latidentatus						5		3		2							2			1
N. multiformis		3		13	3	12	1	14		1		1	1	1	1					22
N. planus				4	6	4	1	28		16		3	3	1	1					
N. subcarnus												1	5	2			41			19
Neoprioniodus spp.	1			8		3		1	2			1	3							1
Neospathognathodus bullatus													1							
N. celloni												1	161	14						
N. pennatus													45	2			2			4
Neospathognathodus? sp.			1																	
Ozarkodina adiutricis													3	6						
O. alisonae												24		3	5	2				
O. cf. O. edithae		1	4	21	1	1	4			3				1						
O gaertneri													104	2			35	5		74
O. hanoverensis													1		1					
O. media		7	1	19	15	3		15	6	8	3	13	9	1			5	1		2
O. typica	1	3	1	6		2	4	3				1								1
Ozarkodina spp.		6	1	10	6	1		1			1	1	2	1						
Paltodus costulatus					3		1			3		1	2				30	3		24
P. debolti	2				12	3	6	39			1									
P. dyscritus	1		2	1	21	4	10	42			3	4	9	1						3
P. migratus	1				13	3	5	27					4							
Panderodus cf. P. gracilis			1	12	24	10	3	19	3		3	7	102							
P. seriatus		13	27	79	7	30		59	3	4	1				2			13		
P. simplex	41	19	59	212	152	28	24	53	27	64	7	75	352	27	20	1	89	20	24	156
P. cf. P. staufferi		2	4	8	20	10		35	8	7	4	7	188				15			21

TABLE IV

Conodont Stratigraphic Ranges: IV

SAMPLE NO. / SPECIES	LLANDOVERY																		lower	
	B$_{1-3}$			C$_{1-2}$					C$_{3-4}$		C$_5$						C$_6$		Wenlock	
	Gelli Farm 1–6	New House, Marshbrook	H. Q. 1, H. Q. 3	Plowden 1–8	Ticklerton Brook	H. V. 3	Minsterley Lane	H. V 4	Norbury 1–3	Sheinton 2	H. B 2	Gullet 1–3	Gullet 4	Hollybush (MB 68/16)	West Malvern 1, 2	Damery Beds	Cowleigh Park 1	Haugh Wood 3	Woolhope 1	Ticklerton 1–3
Panderodus unicostatus	78	19	129	416	[illegible]75	51	27	107	30	181	11	179	1304	51	2[illegible]	7	292	40	91	361
Panderodus sp. A		1		11	7	[illegible]		[illegible]	2	6			41				23	3		16
Plectospathodus extensus				1				25		2	1	1	5				6			
P. flexuosus					4	1	2					1	1							
P. irregularis				2		2			1											
Plectospathodus spp				1									1							
Pt. amorphognathoides																	88	9		77
Pygodus? lyra													20							
Sagittodontus edentatus	5	5	12	2			2			2	9	1		1	4		1			
Spathognathodus abruptus		3	7	16		2														
S. cf. S. abruptus							1													
S. gulletensis										1	1	258	29	8	18	7				
S. hassi		5	1	26		1				1										
S. inclinatus				15		7	1	20	21	7	4	8	23		3	1		1		
S. oldhamensis		10	8	15	18															
S. polinclinatus												1		12						
S. ranuliformis											3	16	18		3	1		1		4
Spathognathodus *n.* sp. A							14													
Spathognathodus *n.* sp. B										5					1					
Spathognathodus spp.		1	2	7		1			3	2				1						
Synprioniodina bicurvata		1					2			2		1	3	1						
S. silurica				1	1						1	4	9	1	1					
Trichonodella asymmetrica				1	1					2	1	2	2							
T. excavata			1	5	1	5		4		2	2	1	17	2			4			5
T? expansa			2	3		3	2			6		7	5	2	1	1				4
T. inconstans		1	7	9	3	4	6	6	2	11	3	2	4	1	2		1			35
T. symmetrica		3	1	1	1		1	9	3		1	21	6	4					1	
Trichonodella spp.		7	3	10	4	6		1	10		4	3	12	1	1					11
gen. et sp. indet. A									1											
gen. et sp. indet. B										1										

Of the platform genera, *Icriodella*, which ranges from the Idwian to the Telychian (C_5), is of particular stratigraphic importance. The stratigraphic distribution and possible phylogenetic relationships of the four species recognized are illustrated in Text-fig. 9. The oldest fauna recovered, probably of early Idwian age, contains *Icriodella discreta*, which is succeeded by *Icriodella deflecta* in the late Idwian. Icriodellids are rare in the C_{1-4} interval of the Welsh Borderland; two broken specimens from the early Fronian are probably referable to *I. deflecta* and two specimens from a horizon of C_{3-4} age are identified as *I.* cf. *I. malvernensis*. The latter appear to be transitional forms in the development of *I. malvernensis* from *I. deflecta*. The genus *Icriodella* is abundant in strata of C_5 age, where it is represented by two species, *I. inconstans* and *I. malvernensis*. *Icriodella inconstans* is the more abundant and widespread, being present in all faunas of C_5 age, whereas *I. malvernensis* is currently known only from the West Malvern locality. No icriodellids have been recovered from strata of younger than C_5 age.

The genus *Icriodina* is morphologically similar to *Icriodella* and the two are possibly phylogenetically related. *Icriodina irregularis* is an important constituent of faunas from the midwestern area of the United States (Rexroad 1967), but is rare in the British collections. A few specimens have been recovered from Idwian and early Fronian strata. A single specimen of *Icriodina* from a younger horizon (Minsterley Lane) is similar in many characteristics to the North American species *I. stenolophata*. These occurrences are depicted in Text-fig. 9.

The genus *Amorphognathus* is represented by a single species, *A. tenuis*, which has been recovered only from strata of late Idwian and early Fronian (C_{1-2}) age. Al-Hasani & Mostler (1969 : text-fig. 12) illustrated an apparent lineage between *Amorphognathus* and *Astropentagnathus*, the latter of which Mostler (1967) considered to be the ancestor of *Apsidognathus* and *Aulacognathus*. A single specimen of *Astropentagnathus irregularis* and several specimens of *Aulacognathus kuehni* and *Apsidognathus tuberculatus* have been recovered from C_5 strata in the Malvern Hills. These occurrences, however, can only be regarded as local and no stratigraphic importance can at present be attached to them. This is also true of the occurrences in C_5 strata of *Astrognathus tetractis*, *Pygodus*? *lyra* and *Ambalodus galerus*. Another possible descendent of *Amorphognathus* is *Hadrognathus staurognathoides*, which is present in small numbers in most samples of C_{3-4} age and younger.

The genus *Neospathognathodus* is important in both the European and North American zonal schemes, but its occurrence may be anomalous in Britain, where it is almost entirely restricted to strata of C_5 age. The species *N. celloni* and *N. pennatus* are common and a single specimen of *N. bullatus* has been recovered. A few specimens of *N. pennatus* occur in C_6 and the early Wenlock. The monospecific genus *Pterospathodus*, which is descended from *Neospathognathodus*, is also stratigraphically important in Europe and North America. In the Welsh Borderland, *Pterospathodus amorphognathoides* is abundant in strata of C_6 and early Wenlock age.

The genus *Spathognathodus* is represented by several species, whose distribution and possible relationships are illustrated in Text-fig. 10. Three species, *S. abruptus*, *S. hassi* and *S. oldhamensis*, are present in the Idwian and range into the Fronian. Morphological similarities between *S. hassi* and *S. oldhamensis* suggest that they

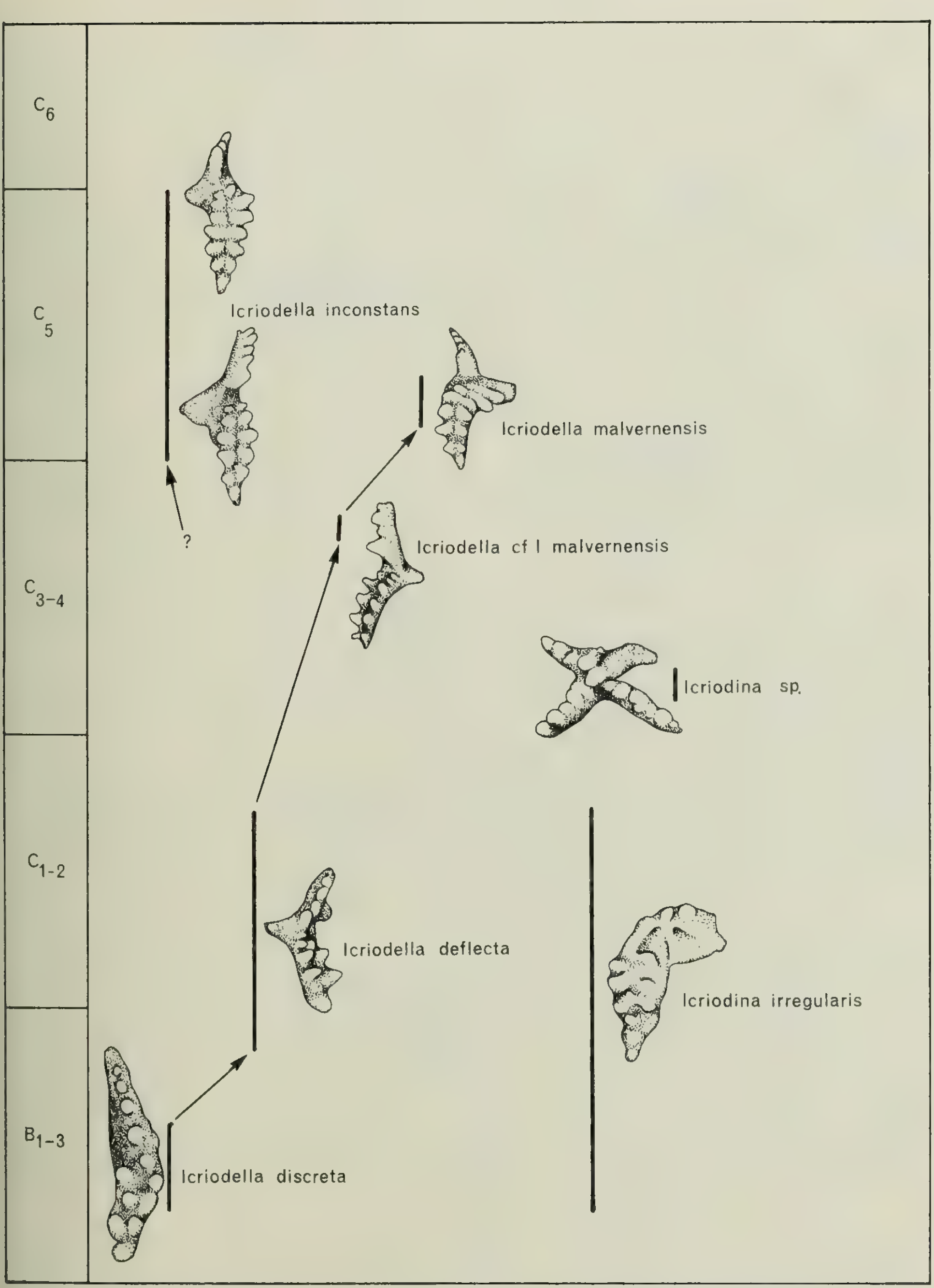


FIG. 9. The genera *Icriodella* and *Icriodina*. Heavy vertical lines indicate approximate stratigraphic ranges. Arrows indicate suggested phylogenetic relationships.

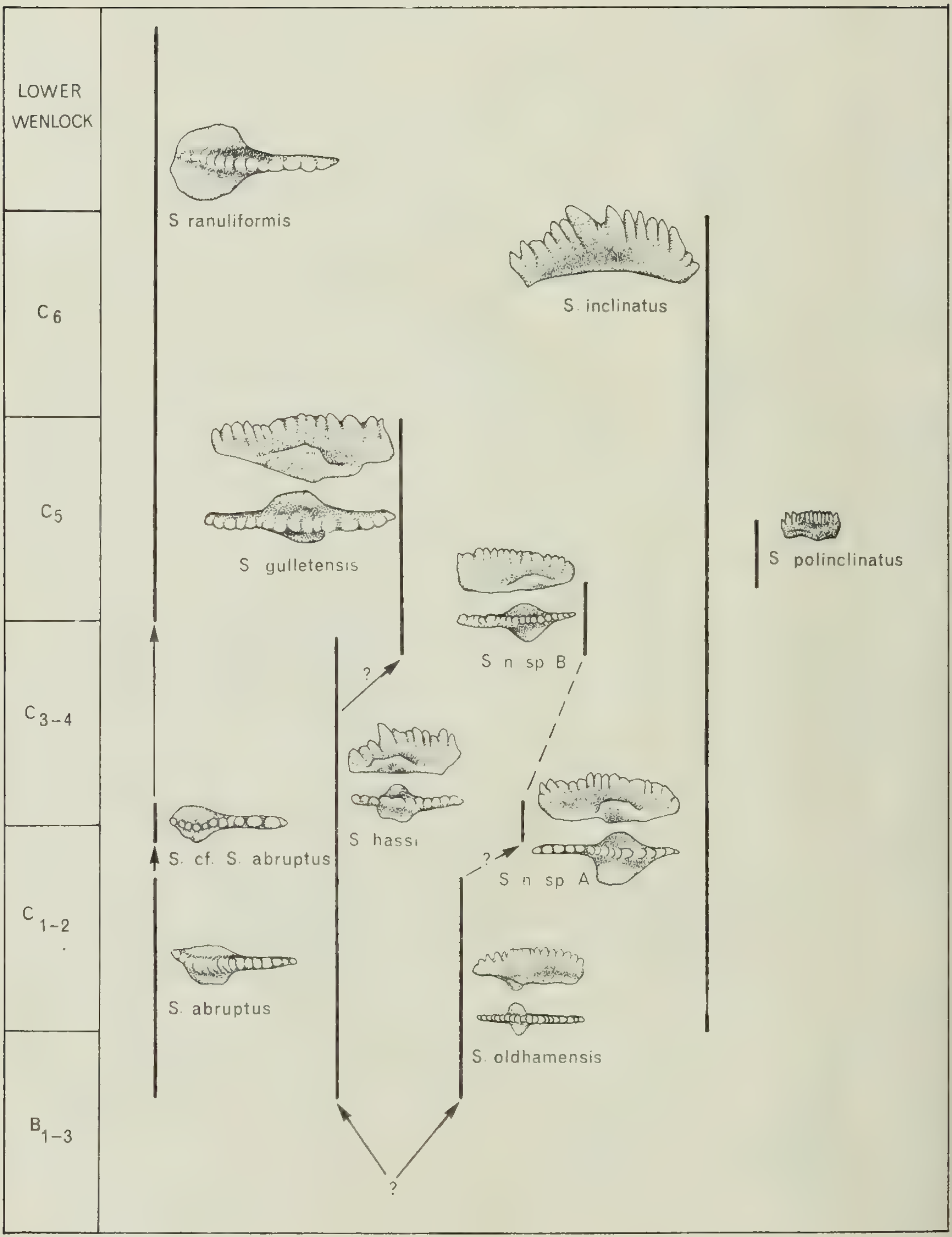


FIG. 10. The genus *Spathognathodus*. Heavy vertical lines indicate approximate stratigraphic ranges. Arrows indicate suggested phylogenetic relationships.

diverged from a common ancestor. *Spathognathodus abruptus* is the probable ancestor of *S. ranuliformis*, an important form in the Telychian and early Wenlock. *Spathognathodus hassi* is possibly ancestral to *S. gulletensis*, which first appears in C_{3-4} and becomes abundant in C_5. *Spathognathodus* n. sp. A, which occurs in a horizon of probable C_{2-4} age, is a possible descendent of *S. oldhamensis*. *Spathognathodus* n. sp. B, of C_{3-5} age, may also be related to these species. *Spathognathodus inclinatus* is common throughout the Fronian and Telychian, but its phylogenetic relationships are obscure. The Llandovery specimens may be homeomorphs of the forms from higher in the Silurian. *Spathognathodus polinclinatus* has been recovered only from C_5 strata and shows no obvious relationship to any other species.

A few species of the bar and blade genera occur in abundance within a limited stratigraphic range. *Ambalodus anapetus* and *Aphelognathus siluricus* are restricted to the late Idwian and early Fronian. *Ozarkodina alisonae* is restricted to C_5, where *O. gaertneri* also makes its first appearance. C_6 and the early Wenlock are characterized by an abundance of diverse species of *Carniodus*, together with *Neoprioniodus subcarnus*, *N. costatus costatus*, *Distomodus triangularis triangularis* and *Exochognathus latialatus*. *Diadelognathus nicolli* has been recovered only from the early Wenlock.

c. Conodont Zones

The stratigraphic distribution of conodonts in the Idwian to early Wenlock strata of the Welsh Borderland allows the recognition of four conodont assemblage zones. These zones, at least in part, are of only local application and the stratigraphic positions of the boundaries between them are known only approximately, because of the widespread nature of the sampling localities. The names proposed for these zones are the *Icriodella discreta—Icriodella deflecta* Assemblage Zone, the *Hadrognathus staurognathoides* Assemblage Zone, the *Icriodella inconstans* Assemblage Zone and the *Pterospathodus amorphognathoides* Assemblage Zone. The stratigraphic ranges and characteristic species of the zones are illustrated in Text-fig. 11.

i. The *Icriodella discreta—Icriodella deflecta* Assemblage Zone

This zone occupies at least the upper part of the Idwian and part of the C_{1-2} interval of the Fronian. The lower limit is unknown, but may be defined at the earliest occurrence of *Icriodella discreta* or *Icriodina irregularis*. The upper limit is defined at the earliest occurrence of *Hadrognathus staurognathoides*.

Icriodina irregularis ranges through the zone, but is rare. The lower part of the zone is characterized by *Icriodella discreta*, the upper part by *Icriodella deflecta*. Several additional species are characteristic of the upper part of the zone, including *Amorphognathus tenuis*, *Spathognathodus abruptus*, *S. hassi*, *S. oldhamensis*, *Ambalodus anapetus*, *Aphelognathus siluricus* and *Exochognathus keislognathoides*.

ii. The *Hadrognathodus staurognathoides* Assemblage Zone

This zone spans an interval from within the upper Fronian (C_{2-3}) to approximately the top of the C_4 division of the Telychian. Graptolites referred to the *turriculatus* Zone have been identified from a horizon within the zone (Cocks & Rickards 1969 :

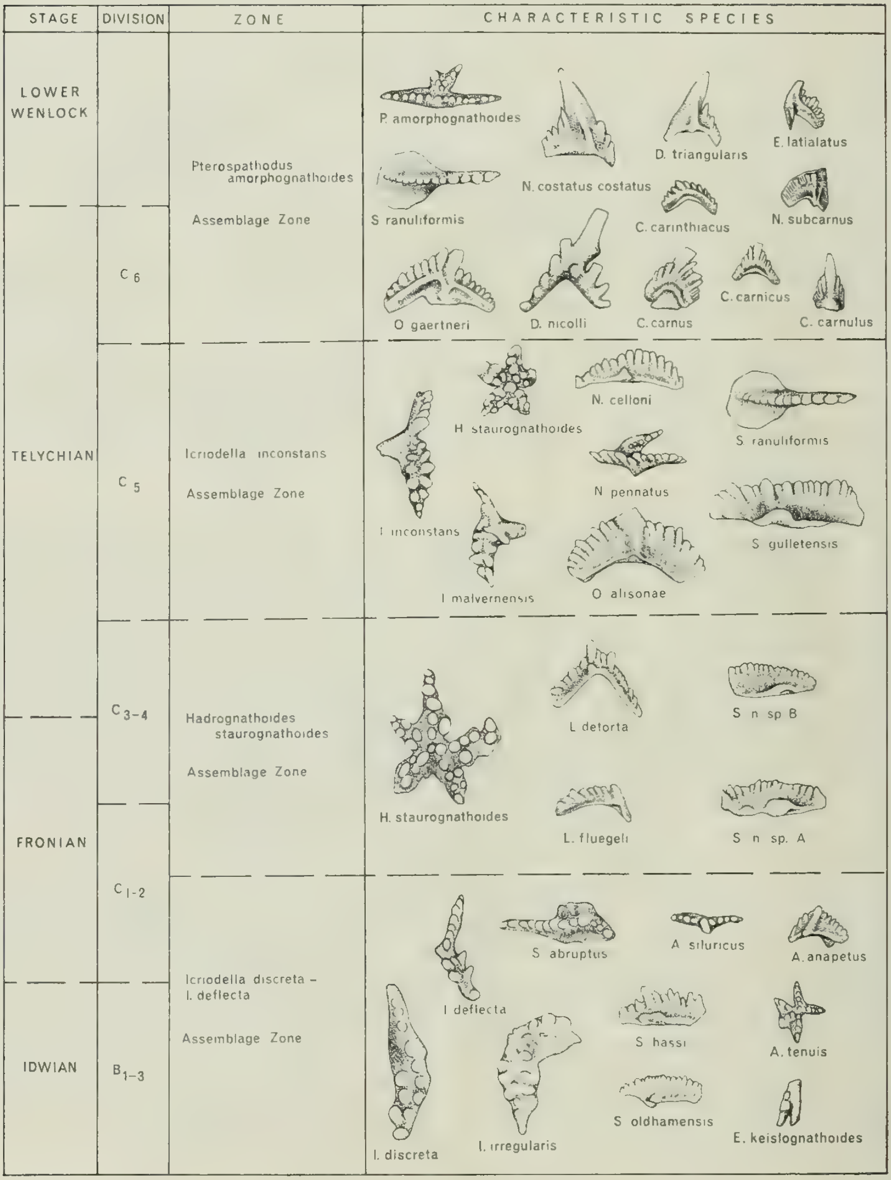

STAGE
DIVISION
ZONE
CHARACTERISTIC SPECIES
LOWER WENLOCK
TELYCHIAN
FRONIAN
IDWIAN
C 6
C 5
C 3-4
C 1-2
B 1-3
Pterospathodus amorphognathoides Assemblage Zone
Icriodella inconstans Assemblage Zone
Hadrognathoides staurognathoides Assemblage Zone
Icriodella discreta – I. deflecta Assemblage Zone
P. amorphognathoides
N. costatus costatus
D. triangularis
E. latialatus
S. ranuliformis
C. carinthiacus
N. subcarnus
O. gaertneri
D. nicolli
C. carnus
C. carnicus
C. carnulus
H. staurognathoides
N. celloni
S. ranuliformis
I. inconstans
N. pennatus
S. gulletensis
I. malvernensis
O. alisonae
L. detorta
S. n. sp. B
H. staurognathoides
L. fluegeli
S. n. sp. A
S. abruptus
A. siluricus
A. anapetus
I. deflecta
S. hassi
A. tenuis
I. discreta
I. irregularis
S. oldhamensis
E. keislognathoides

FIG. 11. Llandovery conodont zones of the Welsh Borderland.

225). The lower limit is defined by the earliest appearance of *Hadrognathus staurognathoides* and the upper limit by the earliest occurrence of *Icriodella inconstans* or *Icriodella malvernensis*. *Hadrognathus staurognathoides* itself ranges far above the upper limit of the zone.

Distinctive forms are few, but *Lonchodina detorta* and *Lonchodina fluegeli* are common. *Spathognathodus* n. sp. A, *Spathognathodus* n. sp. B and forms that appear to be transitional from *Spathognathodus abruptus* to *S. ranuliformis* also occur. It is possible that further collecting may enable better definition of the zone in terms of *Icriodella* or *Spathognathodus*.

iii. The *Icriodella inconstans* Assemblage Zone

This zone is approximately equivalent to the C_5 subdivision of the Telychian. A tie between part of this zone and a horizon in the *greistoniensis* graptolite zone was established by Jones, Brooks, Basset, Austin & Aldridge (1969). The lower limit of the zone is defined at the earliest occurrence of *Icriodella inconstans* or *Icriodella malvernensis*. The upper limit is defined by the earliest occurrence of *Pterospathodus amorphognathoides* in association with other characteristic species of the succeeding zone.

Characteristic species include *Icriodella inconstans*, *I. malvernensis*, *Spathognathodus gulletensis*, *Ozarkodina alisonae*, *Neospathognathodus celloni* and *N. pennatus*. *Spathognathodus ranuliformis* and *Ozarkodina gaertneri* make their first appearances in this zone.

iv. The *Pterospathodus amorphognathoides* Assemblage Zone

This zone is present in at least the upper part of the C_6 subdivision of the Telychian, and extends into the early Wenlock. The lower limit is marked by the earliest occurrence of *Pterospathodus amorphognathoides*. The occurrence of *P. amorphognathoides* in older strata in North America and the European continent was, however, recorded by Nicoll & Rexroad (1968 : 6). In view of this, it is probably advisable to define the lower limit of the *Pterospathodus amorphognathoides* Assemblage Zone at the earliest occurrence of *P. amorphognathoides* in association with other species characteristic of the zone. The upper limit of the zone is unknown and cannot at present be defined.

Species characteristic of this zone are *Pterospathodus amorphognathoides*, *Spathognathodus ranuliformis*, *Ozarkodina gaertneri*, *Carniodus carinthiacus*, *C. carnicus*, *C. carnulus*, *C. carnus*, *Distomodus triangularis triangularis*, *Diadelognathus nicolli*, *Exochognathus latialatus*, *Neoprioniodus subcarnus* and *N. costatus costatus*.

d. Correlation with Europe and North America

The approximate relationships between the zones recognized in the Welsh Borderland and those erected in Europe by Walliser (1964) and in North America by Nicoll & Rexroad (1968) are tabulated in Text-fig. 12. The local stratigraphic ranges of several species are affected by faunal province or facies control, and this is a complicating factor in correlation. In the present state of knowledge there is sufficient evidence for several broad intercontinental correlations to be suggested.

CARNIC ALPS Walliser (1964)	INDIANA AND KENTUCKY Nicoll & Rexroad (1968)	WALES AND THE WELSH BORDERLAND
amorphognathoides-Zone	*Pterospathodus amorphognathoides* – *Spathognathodus ranuliformis* Assemblage Zone	*Pterospathodus amorphognathoides* Assemblage Zone
	Neospathognathodus celloni Assemblage Zone	*Icriodella inconstans* Assemblage Zone
celloni-Zone		
		Hadrognathus staurognathoides Assemblage Zone
Bereich 1 (upper part)	*Icriodina irregularis* Assemblage Zone	*Icriodella discreta* – *Icriodella deflecta* Assemblage Zone

FIG. 12. Approximate relationships between the European, American and British Llandovery conodont zones.

The *Icriodella discreta—Icriodella deflecta* Assemblage Zone is approximately equivalent to the *Icriodina irregularis* Assemblage Zone of North America. The upper limits of the zones are defined differently, due to the apparently locally restricted ranges of *Neospathognathodus* and *Ozarkodina adiutricis* in Britain. On a broad scale the two zones may be regarded as equivalent. Due to faunal provincialism, *Icriodina* is replaced by *Icriodella discreta* and *Icriodella deflecta* in the lower Silurian of northern Michigan and Ontario (Pollock, Rexroad & Nicoll 1970). The ornamentation of the fragments of *Icriodella* illustrated by Walliser (as *Icriodina irregularis*) is similar to that displayed by *I. deflecta* and *I. discreta* and the upper part of Walliser's Bereich I interval in the Carnic Alps possibly correlates with the *Icriodella discreta—Icriodella deflecta* Assemblage Zone of Britain.

Formations referred to the *Icriodina irregularis* Assemblage Zone of North America or the upper part of Bereich I in Europe are considered to be of similar age to the Idwian and early Fronian strata of Britain. These formations include the Brassfield Formation of midwestern America (Branson & Branson 1947, Rexroad 1967), exclusive of the Lee Creek Member at the top (Nicoll & Rexroad 1968). The conodont faunas of the Manitoulin Dolomite and Cabot Head Shale of northern Michigan and Ontario (Pollock, Rexroad & Nicoll 1970) are similar in age and faunal province to the British faunas. The Neahga Shale of the Niagara Gorge section also contains abundant icriodellids (Rexroad & Rickard 1965 : 1220) and was placed in the *Icriodina irregularis* Assemblage Zone by Pollock *et al.* (1970). *Icriodella* is present in all but the lower part of the 'Untere Schichten' of the Cellon section in the Carnic Alps (Walliser 1964).

The *Hadrognathus staurognathoides* Assemblage Zone is an interval poor in stratigraphically useful conodonts, occurring above the distinctive fauna of the *Icriodella discreta—Icriodella deflecta* Assemblage Zone and below the *Icriodella inconstans* Assemblage Zone, in which *Neospathognathodus* first appears. In Europe there is no recorded gap between *Icriodella* and *Neospathognathodus*, and in North America the ranges of *Icriodina* and *Neospathognathodus* overlap (Nicoll & Rexroad 1968 : 6; Craig 1969 : 1626). *Hadrognathus staurognathoides* and *Lonchodina fluegeli* first appear at the base of the *celloni*-Zone in Europe (Walliser 1964 : table 2) and it is very possible that the *H. staurognathoides* Assemblage Zone is equivalent to the lower part of the *celloni*-Zone and that *Neospathognathodus celloni* and *Ozarkodina adiutricis* are absent because of facies control or faunal provincialism. Rexroad (*in* Craig 1969 : 1625) has suggested that the *celloni*-Zone in Europe may be bounded by unconformities, and if this is the case the *Hadrognathus staurognathoides* Assemblage Zone could occupy an interval that is not represented in the Carnic Alps. The fact that the *celloni*-Zone occupies less than three metres of strata in the Cellon section indicates that the sequence may be considerably condensed. The Lee Creek Member of the Brassfield Limestone of North America is only one metre thick, but contains the entire stratigraphic range of the *Neospathognathodus celloni* Assemblage Zone of Nicoll & Rexroad (1968). It is possible that the *Hadrognathus staurognathoides* Assemblage Zone of the Welsh Borderland is represented by such a small thickness of strata elsewhere that it has not been differentiated.

Many diagnostic species of the *Icriodella inconstans* Assemblage Zone have not been recorded outside Britain and cannot, as yet, be applied to international correlation. The zone contains elements of both the *celloni*-Zone and the *amorphognathoides*-Zone of Europe, *Neospathognathodus celloni*, for example, being associated with *Ozarkodina gaertneri* and *Spathognathodus ranuliformis*. Nicoll & Rexroad (1968 : 6) recorded a similar overlap of Walliser's guide species, but in North America it is *Pterospathodus amorphognathoides* that is associated with species of *Neospathognathodus*. The suggestion by Rexroad (*in* Craig 1969 : 1625) that there may be an unconformity between Walliser's zones is a possible explanation of the mutually exclusive ranges of zonal species in the Carnic Alps. The *Icriodella inconstans* Assemblage Zone is probably equivalent to the upper part of Walliser's *celloni*-Zone and may include the lower part of his *amorphognathoides*-Zone. There is correlation with at least the upper part of the *Neospathognathodus celloni* Assemblage Zone of North America. At least the upper part of the Lee Creek Member of the Brassfield Limestone, therefore, appears to be of C_5 age. Unconformities in the Niagara Gorge section (Rexroad & Rickard 1965 : 1219) and in northern Arkansas (Craig 1969 : 1624) at least partially encompass this interval. Beds of C_5 age are probably present within the 'Trilobiten und Aulacopleura Schichten' of the Carnic Alps, either side of the boundary between Walliser's *celloni*- and *amorphognathoides*-Zones.

The *Pterospathodus amorphognathoides* Assemblage Zone of the Welsh Borderland is of particular importance, as it traverses the Llandovery/Wenlock boundary. It is approximately equivalent to the *Pterospathodus amorphognathoides—Spathognathodus ranuliformis* Assemblage Zone of North America and to the *amorphognathoides*-Zone of Europe. North American strata containing conodonts indicative of the level include the lower part of the Osgood Member of the Salomonie Dolomite of Indiana and Kentucky (Nicoll & Rexroad 1968 : 3), the upper part of the Cason Shale and the lower part of the St. Clair Limestone of northern Arkansas (Craig 1969 : fig. 1) and the Rockway Dolomite Member of the Irondequoit Limestone in the Niagara Gorge (Rexroad & Rickard 1965 : fig. 1). The Llandovery/Wenlock boundary at the latter locality may be within the Rockway Dolomite or it may be within the interval represented by the unconformity at the base of the dolomite. The Llandovery/Wenlock boundary in the Cellon section of the Carnic Alps can be placed within that part of the 'Trilobiten-und-Aulacopleura Schichten' that is referred to the *amorphognathoides*-Zone. The *amorphognathoides*-Zone at this locality occupies less than two metres of strata.

e. Faunal Provincialism

The restriction of some lower Silurian conodont species to faunal provinces was first reported by Nicoll & Rexroad (1968 : 6), who noted that *Icriodina*, which was common in the Cincinnati Arch area, appeared to be absent from the Silurian sections of the Niagara Gorge and Europe, where it was replaced by *Icriodella*. They also noted that several species that were common in North America were not recorded by Walliser from the Carnic Alps.

Faunal provincialism in the *Icriodina irregularis* Assemblage Zone of North America was discussed by Pollock, Rexroad & Nicoll (1970), who recognized different provinces in the Cincinnati Arch area of midwestern America and in the northern Michigan and Ontario area. As well as the replacement of *Icriodina* by *Icriodella* in the northern area, several differences were noted at the species level. In particular, *Aphelognathus siluricus* and *Ambalodus anapetus* were present only in the northern area. *Spathognathodus* was more abundant in the north, where it was represented by a greater variety of species. In all, 22 species were recorded only from the northern area and 12 occurred only in the midwestern area.

Faunas of similar age from the Welsh Borderland show a much closer similarity to those of the northern area than to those of the midwestern area. *Icriodella discreta* and *I. deflecta* are the dominant platform elements and *Icriodina irregularis* is rare. *Aphelognathus siluricus* is present and *Ambalodus anapetus* is abundant. The genus *Spathognathodus* is represented by three common species, *S. hassi*, *S. oldhamensis* and *S. abruptus*. *S. hassi* and *S. oldhamensis* occur in both North American provinces. *S. abruptus* may be a geographic variant of *S. manitoulinensis*, which is present only in the northern province of America. Of the other species recorded only in the northern area by Pollock *et al.* (1970 : table 1), *Ligonodina silurica*, *Neoprioniodus planus*, *Plectospathodus flexuosus*, *Synprioniodina silurica* and *Trichonodella symmetrica* are present, but rare, in the British faunas. Of the species recorded only in the midwestern area, *Icriodina irregularis*, *Exochognathus* (*Rhynchognathodus*?) n. sp., *Distomodus*? *extrorsus* and *Plectospathodus irregularis* are present, but rare, in the British faunas. *Icriodina* and *Icriodella* have not previously been definitely recorded in association. On this evidence, the British faunas show a link with the northern province of North America, but there is some admixing of forms characteristic of the southern area. The species *Sagittodontus robustus*, *Spathognathodus comptus* and *S. elibatus* which are common in the northern province of America, are absent from the Welsh Borderland collections. *Amorphognathus tenuis*, which is an important constituent of the British faunas, has not been recorded in North America.

The upper part of Bereich I in Europe is characterized by *Icriodella*, in association with *Amorphognathus* and *Ambalodus triangularis* (Walliserj1964). Walliser recorded only eight species in this interval and, although simple cones were not included, this is very few in comparison with the number present in time-equivalent strata in Britain and North America. Whether this low diversity is due to faunal provincialism, local facies control, post-mortem sorting or some other factor cannot at present be determined.

No significant differences were recorded by Pollock *et al.* (1970 : 745) in the *Neospathognathodus celloni* and *Pterospathodus amorphognathoides—Spathognathodus ranuliformis* Assemblage Zones of the northern and midwestern areas. There are, however, several notable differences between the faunas from this interval in the United States and in the Carnic Alps. The European species *Ambalodus galerus*, *Astrognathus tetractis* and *Pygodus*? *lyra* have not been recorded in North America. *Astropentagnathus irregularis* and *Spathognathodus tyrolensis*, described from Austria by Mostler (1967), are also absent from known American faunas. Species described from North America that have not been recorded from the European continent include all the known species of *Diadelognathus*, together with *Distomodus kentucky-*

ensis, *Exochognathus brassfieldensis*, *Icriodina stenolophata*, *Neospathognathodus bullatus*, *N. ceratoides*, *N. latus*, *Ozarkodina hanoverensis*, *Sagittodontus edentatus*, *Spathognathodus polinclinatus* and *Trichonodella*? *expansa*. Several of these species are very abundant in North America and faunal provincialism may explain their absence from the European collections.

In Britain, there is some intermixing of European and American forms, in association with several new forms whose known occurrence is at present restricted to the Welsh Borderland. *Diadelognathus* occurs sporadically and *Distomodus kentuckyensis*, *Exochognathus brassfieldensis*, *Sagittodontus edentatus* and *Trichonodella*? *expansa* are common, indicating a similarity to the American faunas. With these, in strata of C_5 age, is associated a great variety of species, including *Ambalodus galerus*, *Apsidognathus tuberculatus*, *Astrognathus tetractis*, *Astropentagnathus irregularis*, *Aulacognathus kuehni*, *Neospathognathodus bullatus*, *Pygodus*? *lyra* and *Spathognathodus polinclinatus*. This association indicates a considerable intermixing of North American and European provincial forms. This intermixing may be taking place within a third province, characterized by *Icriodella inconstans*, *I. malvernensis*, *Spathognathodus gulletensis* and *Ozarkodina alisonae*. It thus appears possible to recognize three provinces in upper *N. celloni* Zone times, a North American province a European province and a British province. The British province contains several species of restricted geographic occurrence, but is also characterized by an intermixing of important species that are mutually excluded from the other two provinces. The extent and nature of the Llandovery faunal provinces are unknown and they may be due to some physical barrier to migration, to climatic control, to sea-depth control or to some other factor.

Of particular interest in the Welsh Borderland is the occurrence of *Spathognathodus ranuliformis* in association with *Neospathognathodus celloni* in strata of C_5 age. Walliser (1964 : table 2) recorded the earliest occurrence of *S. ranuliformis* in the Carnic Alps at a level above the base of the *amorphognathoides*-Zone. Similarly, Nicoll & Rexroad (1968 : 8) noted that *S. ranuliformis* was generally found higher in the *P. amorphognathoides—S. ranuliformis* Assemblage Zone than any other of the characteristic species. It is possible that *S. ranuliformis* represents a species which first appeared in the British province and migrated at a later date into the North American and European provinces. Other forms characteristic of the British province in C_5 times may have become extinct before such migration became possible.

f. Facies Control

A full appreciation of facies control requires a comparative study of a large number of collections from widespread localities where detailed information concerning facies is available. Such a wide synthesis is outside the scope of this study, but some effects of facies control on local distribution can be appreciated. The animal communities defined by Ziegler, Cocks & Bambach (1968) provide useful information about the depth of the sea in which Llandovery sediments accumulated. These communities have been recognized at many localities in Wales and the Welsh Borderland by Ziegler, Cocks & McKerrow (1968). Several of the samples collected during the present investigation are from these localities and the animal communities are known. Comparisons can, therefore, be made between faunas of similar age that occur in sediments deposited in different sea-depths.

Of the collections referred to the *Icriodella discreta—Icriodella deflecta* Assemblage Zone, three are from localities where the animal community is known. The Pentamerus Beds of New House, Marshbrook, contain a mixed *Lingula/Rostricellula*? community, while those of Plowden contain a *Pentamerus* community (Ziegler, Cocks & McKerrow 1968 : 746). The Venusbank Formation at Hope Quarry contains a *Stricklandia* community (Ziegler *et al.* 1968 : 743). There are several minor differences in the faunas, all of which could be accounted for by the restrictions of sampling. A major trend, however, is apparent in the species *Amorphognathus tenuis* and *Ambalodus anapetus*, which are abundant in the shallow water fauna of New House, Marshbrook. These two species are present, but in much smaller numbers, in the deeper water fauna of Plowden and they are totally absent from the collections from Hope Quarry. It is possible that *Amorphognathus tenuis* and *Ambalodus anapetus* are restricted to a shallow water facies, although other factors, such as post-mortem sorting, could account for their distribution. Simple cones are much more abundant in the collections from deeper water sediments than in those from shallow water. In the New House, Marshbrook collection 16% of the specimens are simple cones, in the Plowden collections the figure is 63% and in the Hope Quarry fauna, 66%.

The *Icriodella inconstans* Assemblage Zone is the only other interval within which several collections of known animal community have been examined. The variety of species at this level is so great that it is difficult to differentiate any definite trends from the variation due to sampling restrictions. In addition to this, several samples are from a high-energy environment and post-mortem sorting has obviously affected conodont distribution. However, some general observations may be made. The zonal species, *Icriodella inconstans*, appears to be independent of sea-depth, occurring in samples from *Costistricklandia*, *Pentameroides* and *Eocoelia* communities as well as in samples in which the brachiopod fauna is a mixture of soft bottom and rocky bottom forms. The unique occurrence of *Icriodella malvernensis* at the West Malvern locality may be due to facies or ecological control, although this does not appear to be related to sea depth. As in the *Icriodella discreta—I. deflecta* Assemblage Zone, the simple cones are much more abundant in the deeper water collections. For example, in Gullet Quarry a progressive increase in depth up the section is indicated by the animal communities. The percentages of simple cones at the sampling horizons are as follows: Gullet 1 18%, Gullet 2 13%, Gullet 2A 70%, Gullet 3 66%, Gullet 4 70%. In the shallow water conglomerates of West Malvern the percentage is 28% and in the *Eocoelia* community at Hollybush Quarry simple cones comprise 40% of the fauna. This evidence suggests a direct or indirect relationship between increasing sea depth and abundance of simple cones in the Llandovery of the Welsh Borderland.

g. Homeomorphy

Homeomorphy in Silurian conodonts was comprehensively discussed by Walliser

(1964 : 20–22) and only a few observations need be stated here. Convergent homeomorphy is apparent in the outline and arrangement of the processes of *Aulacognathus kuehni* (Pl. 2, fig. 6) and the holotype of *Kockelella patula* (Walliser 1964 : pl. 15, fig. 16). The two Llandovery species *Aphelognathus siluricus* (Pl. 3, fig. 13) and *Neospathognathodus celloni* (Pl. 3, figs 9–12) are also closely similar.

It is important that the frequent occurrence of homeomorphy is borne in mind when isolated conodont faunas are under examination. In particular, failure to recognize those forms which periodically split off from a common antecedent and morphologically similar forms that are separated by a morphologically distinct intermediate form could lead to incorrect stratigraphic interpretation. In view of this, some genera and species from this study whose stratigraphic range is not known to be continuous with similar forms of older or younger age must be regarded as possible homeomorph forms. Pollock, Rexroad & Nicoll (1970 : 754) suggested that, as a continuous lineage has not been recognized, the lower Silurian specimens referred to *Icriodella* may be homeomorphs of those from the Ordovician. Other Llandovery conodonts that are possibly homeomorphs of Ordovician forms include *Panderodus* cf. *P. gracilis*, *Panderodus* cf. *P. staufferi* and the genera *Pygodus*? and *Gothodus*?. Forms that may be homeomorphs of younger Silurian species include those referred to *Ozarkodina* cf. *O. edithae*, *Ozarkodina typica* and *Spathognathodus inclinatus*.

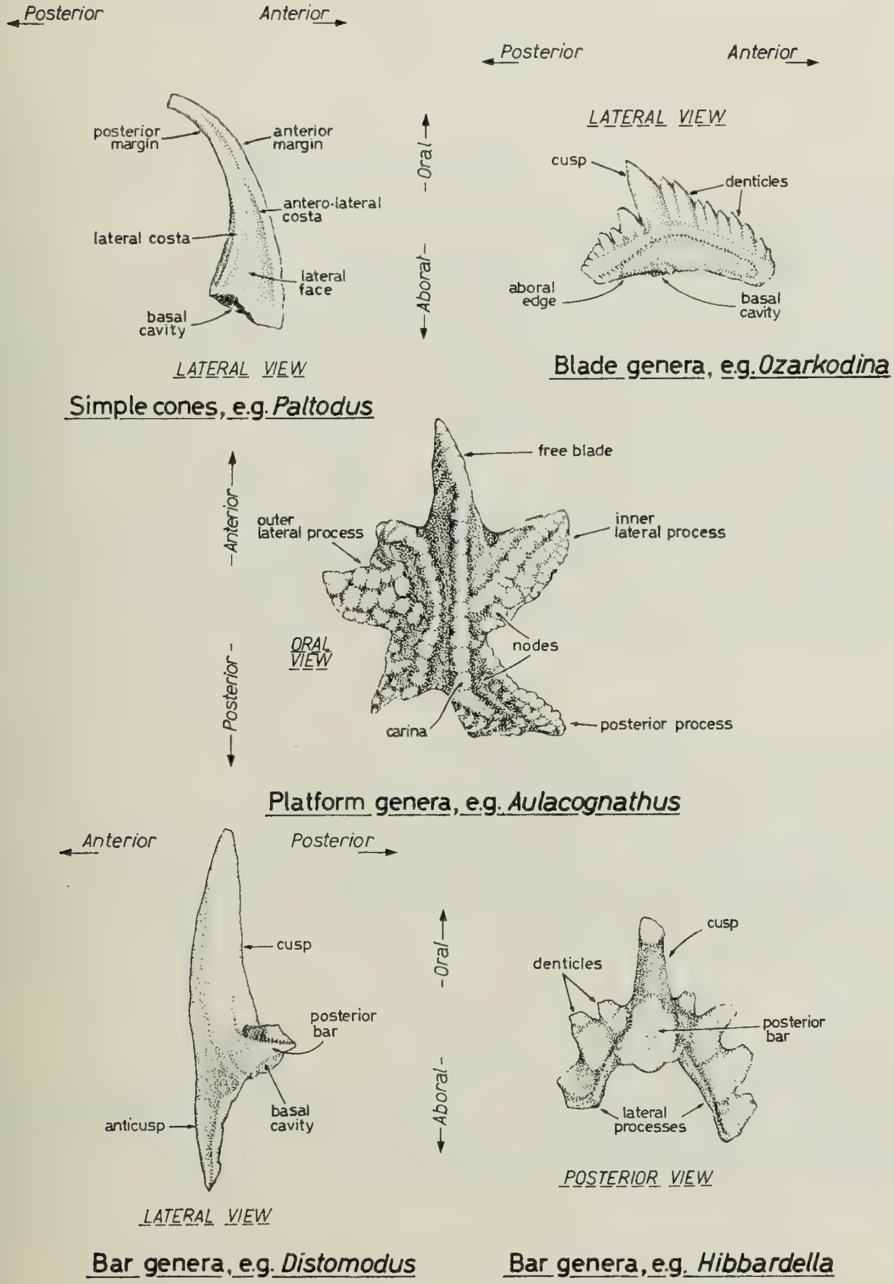
VI. SYSTEMATIC PALAEONTOLOGY

In the erection of new species care has been taken to distinguish between the two procedures of naming and definition. A single specimen of a sampled population has been selected as a named holotype and, as stressed by Simpson (1961 : 30), that name belongs to the species in which the type specimen is placed. The holotype is in no way considered to be morphologically 'typical' of the species to which it belongs. Study of the variation of statistically significant populations from varied ecological and geographical localities is necessary to satisfactorily define a species, and in this respect it is considered misleading to designate selected 'paratypes', which cannot adequately represent a whole population (see Simpson 1961 : 47 for detailed argument).

In consideration of subspecies, only those that are geographically or successionally isolated are valid in evolutionary theory. Where previous authors have defined, within a single species, subspecies that occur at the same locality and horizon, the subspecific status is considered invalid (see Sylvester-Bradley 1956 : 3). In such cases, the taxa are either combined as a single species or given separate specific status.

The morphological terminology and orientation employed in the systematic descriptions of this section are illustrated in Text-fig. 13. The occurrences of species are given for the Welsh Borderland within the stratigraphic range Idwian to early Wenlock, although many species are known to have a stratigraphic range that extends beyond these limits.

The repository of the figured specimens (pre-fixed X.) is the British Museum (Natural History). The remainder of the collections are deposited at the Department of Geology, University of Southampton.


Posterior
Anterior
posterior margin
anterior margin
antero-lateral costa
lateral costa
lateral face
basal cavity
LATERAL VIEW
-Oral-
-Aboral-
Posterior
Anterior
LATERAL VIEW
cusp
denticles
aboral edge
basal cavity
free blade
-Anterior-
outer lateral process
inner lateral process
ORAL VIEW
nodes
-Posterior-
carina
posterior process
Anterior
Posterior
cusp
posterior bar
basal cavity
anticusp
LATERAL VIEW
-Oral-
-Aboral-
cusp
denticles
posterior bar
lateral processes
POSTERIOR VIEW

Simple cones, e.g. *Paltodus*

Blade genera, e.g. *Ozarkodina*

Platform genera, e.g. *Aulacognathus*

Bar genera, e.g. *Distomodus*

Bar genera, e.g. *Hibbardella*

FIG. 13. Morphological terminology and orientation.

Genus *ACODUS* Pander, 1856

TYPE SPECIES. *Acodus erectus* Pander, 1856.

Acodus curvatus Branson & Branson

Plate 9, fig. 1

1947 *Acodus curvatus* Branson & Branson: 554, pl. 81, fig. 20.
1964 *Acodus* cf. *mutatus* (Branson & Mehl) Serpagli & Greco: 196, pl. 34, figs 2a, b.
1967 *Acodus curvatus* Branson & Branson; Rexroad: 25, pl. 4, figs 9–12.
1968 *Acodus curvatus* Branson & Branson; Nicoll & Rexroad: 23, pl. 7, figs 19, 20.
1970 *Acodus curvatus* Branson & Branson; Pollock, Rexroad & Nicoll: 749, pl. 114, fig. 35.

MATERIAL. 86 specimens: figured (X.708).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cone is curved, often strongly, at midlength and the apical portion is commonly twisted inwards. The anterior and posterior edges are sharp. The outer lateral face is convex and usually unornamented, but a poorly developed costa may be present. The inner lateral face is slightly convex and bears a small costa, situated posterior of centre. The unit is laterally compressed and the outline of the base is lenticular. The entire base is excavated, the cavity extending for half the length of the cone.

Acodus unicostatus Branson & Branson

Plate 9, figs 2, 3

1947 *Acodus unicostatus* Branson & Branson: 554, pl. 82, figs 9, 10, 41, 43.
1947 *Paltodus acostatus* Branson & Branson (*partim*): 554, pl. 82, figs 23, 24 only.
1967 *Acodus unicostatus* Branson & Branson; Rexroad: 26, pl. 4, figs 13–16.
1968 *Acodus unicostatus* Branson & Branson; Nicoll & Rexroad: 23, pl. 7, figs 34–36.
1970 *Acodus unicostatus* Branson & Branson; Pollock, Rexroad & Nicoll: 749, pl. 114, figs 36, 37.

MATERIAL. 185 specimens: figured (X.709), (X.710).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is curved and asymmetrical. The posterior edge is sharp. One lateral face is flat or gently convex, the other is strongly convex with a well-developed medial costa. The entire base is excavated and the cavity extends for one-third to two-thirds of the length of the cone.

Genus *AMBALODUS* Branson & Mehl, 1933

TYPE SPECIES. *Ambalodus triangularis* Branson & Mehl, 1933.

Ambalodus anapetus Pollock, Rexroad & Nicoll

Plate 3, fig. 4

1970 *Ambalodus anapetus* Pollock, Rexroad & Nicoll: 749, pl. 112, figs 9–15.

MATERIAL. 132 specimens: figured (X.619).

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The short, stout cusp is situated at the apex of the unit and supports denticulate anterior and posterior processes, which flare downwards to give a wide base. The processes bear small denticles that may be discrete or fused nearly to the tips. Either process may be longer than the other, or they may be of equal length. The outer lateral face of the apical denticle gives rise to a low ridge, directed slightly anteriorly. This rudimentary outer lateral process is usually unornamented, but may be serrated. Some specimens also bear a small serrated ridge on the posterior portion of the inner lateral face. The entire aboral surface is deeply excavated.

Ambalodus galerus Walliser

Plate 3, figs 6, 8

1964 *Ambalodus galerus* Walliser: 27, pl. 6, fig. 1; pl. 12, figs 1–7.
1968 *Ambalodus galerus* Walliser; Igo & Koike: 7, pl. 2, fig. 23.

MATERIAL. 44 specimens: figured (X.622), (X.623).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The strongly developed cusp is situated at the apex of the unit and supports denticulate anterior and posterior processes. The unit is widely flared at the base. The anterior process bears denticles that are almost totally fused to form a jagged ridge; the posterior process is shorter, lower and less well-developed. In oral view, the angle between the two processes is about 170°. The outline of the base is an irregular ellipse and the basal edge of some specimens is tuberculate. The deeply excavated aboral surface often contains basal material.

Ambalodus spp.

Plate 3, figs 5, 7

11 specimens of *Ambalodus*, not referable to the species described above, have been recovered from strata of Idwian and Fronian age. Included here is a pyramidal form with a stout apical denticle (Pl. 3, fig. 5). 4 specimens from Ticklerton Brook appear to be referable to *A. triangularis* Branson & Mehl (Pl. 3, fig. 7), but these may not be indigenous.

Genus *AMORPHOGNATHUS* Branson & Mehl, 1933

TYPE SPECIES. *Amorphognathus ordovicica* Branson & Mehl, 1933.

Amorphognathus tenuis sp. nov.

Plate 2, figs 3, 4

Derivation of name. Latin, thin.

Diagnosis. *Amorphognathus* Branson & Mehl in which the anterior and posterior processes together form a slightly curved blade, which supports a bifurcating inner lateral process and a blade-like outer lateral process.

Holotype. Specimen (X.572).

Material. *ca.* 60 specimens: figured (X.572), (X.573).

Type locality and horizon. Pentamerus Beds, Plowden, Shropshire. Sample Plowden 3.

Occurrence. Late Idwian and early Fronian.

Description. The slightly curved antero-posterior blade bears up to 15 laterally compressed denticles and may be a little expanded in the posterior half. A denticle near the midlength of the blade is slightly higher than its neighbours, forming a small cusp. The bifurcating inner lateral process is situated at, or just posterior to, midlength of the unit. The anterior branch of the process is the longer, bearing three to five sharp denticles and forming an angle of about 50° with the blade. The posterior branch of the process forms a similar angle with the blade and bears two or three denticles. The outer lateral process is situated at, or just anterior to, midlength of the unit and is never directly opposite the inner lateral process. It consists of a single, somewhat posteriorly bent branch, which is approximately perpendicular to the blade and bears up to six denticles. The denticle row of the outer lateral process may be connected to the cusp by a low costa. A wide basal cavity is excavated beneath the blade and the processes.

Remarks. In most descriptions of species of *Amorphognathus* mention has been made of the delicate nature of the specimens and the consequent rarity of complete, well-preserved examples. This is also true of the present material, and the presence of a large number of fragments probably representing parts of *A. tenuis* sp. nov. makes the estimation of true abundance impossible. The totals given herein are based only on the more complete specimens.

Bergström (1964 : 13–14) discussed the apparent dimorphism shown by species of *Amorphognathus* with special reference to *A. ordovicicus* Branson & Mehl. The latter species includes forms with an anterior blade that is continued as a platform-like posterior process ('blade' type) and forms in which both the anterior and posterior processes are expanded into a platform ('non-blade' type). The present specimens show no marked dimorphism, both processes being bladelike in all cases, although in a few examples the posterior process is slightly expanded.

Genus ***APHELOGNATHUS*** Branson, Mehl & Branson, 1951

Type species. *Aphelognathus grandis* Branson, Mehl & Branson, 1951.

Aphelognathus siluricus Pollock, Rexroad & Nicoll

Plate 3, fig. 3

1970 *Aphelognathus siluricus* Pollock, Rexroad & Nicoll: 749, pl. 114, figs 1–4.

MATERIAL. 30 specimens: figured (X.618).

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The slightly bowed blade bears a row of 11 to 14 small denticles of subequal size. In lateral view, the denticle row forms an arc. The lateral faces diverge towards the base and flare out near the midpoint on each side to form slightly offset lateral processes, which are short and unornamented. The entire aboral surface is deeply excavated.

REMARKS. The morphology of this species is similar to that of the combined anterior and posterior processes of *Amorphognathus tenuis* The lateral processes of *A. siluricus*, however, project only a short distance laterally and are unornamented. There is a possibility of confusion between broken specimens of the two species.

A morphological resemblance also exists to *Neospathognathodus celloni*, which is also a blade form with offset, unornamented lateral processes. The wide, deep basal cavity of *A. siluricus* serves to distinguish the two species.

Genus ***APSIDOGNATHUS*** Walliser, 1964

TYPE SPECIES. *Apsidognathus tuberculatus* Walliser, 1964.

Apsidognathus tuberculatus Walliser

Plate 2, figs 7, 9

1964 *Apsidognathus tuberculatus* Walliser: 29, pl. 5, fig. 1; pl. 12, figs 16–22; pl. 13, figs 1–5.
1968 *Apsidognathus tuberculatus* Walliser; Nicoll & Rexroad: 24, pl. 3, fig. 8.

MATERIAL. 61 specimens: figured (X.593), (X.594).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The short free blade continues as a prominent curved carina more or less medially over the arched platform. Two rows of nodes diverge from the carina on each side, but do not form well-marked lateral processes. The oral surface between the rows of nodes is generally ornamented by tubercles, arranged concentrically and parallel to the irregular margin of the platform. In mature specimens the coarse development of these tubercles may mask the pattern of the lateral nodose rows. The aboral surface is deeply excavated and commonly contains basal material.

Genus ***ASTROGNATHUS*** Walliser, 1964

TYPE SPECIES. *Astrognathus tetractis* Walliser, 1964.

DIAGNOSIS. The unit consists of a basally excavated blade, bearing a lateral process on each side. The two lateral processes are situated directly opposite one another and each forms an angle of approximately 90° with the blade.

REMARKS. Walliser (1964 : 30) erected the genus *Astrognathus* for four specimens, and in diagnosis stated that these conodonts comprised four processes of equal length. Specimens from this study possess lateral processes that do not arise from the mid-point of the blade and the four processes are, therefore, of unequal length. These specimens indicate a greater range of variation for the genus. In view of this, the diagnosis has been emended and the revised version is given above.

Astrognathus tetractis Walliser

Plate 3, fig. 1

1964 *Astrognathus tetractis* Walliser: 30, pl. 5, fig. 4; pl. 14, figs 1, 2.

MATERIAL. 16 specimens: figured (X.608).

OCCURRENCE. Telychian (C_5).

DIAGNOSIS. The genus is at present monospecific and the emended diagnosis for the genus also applies to this species.

DESCRIPTION. A slightly arched blade, bearing fused denticles of equal size, supports a lateral process on each side. The two processes are perpendicular to the blade and are situated opposite each other. The processes bear fused denticles of equal size and together form an arch, which is steeper than that of the blade. In most specimens the processes arise from a point up to two-thirds along the length of the blade and can be clearly distinguished. The basal cavity, which is enlarged beneath the junction of the processes, continues only under the blade.

REMARKS. These specimens differ from those described by Walliser (1964) in that the blade and the lateral processes can be clearly distinguished in oral view. Aborally, the blade of all specimens can be distinguished by the extension of the basal cavity along it. The present specimens resemble the formerly described specimens of *A. tetractis* in all other characteristics and are considered conspecific with them.

Genus ***ASTROPENTAGNATHUS*** Mostler, 1967

TYPE SPECIES. *Astropentagnathus irregularis* Mostler, 1967.

Astropentagnathus irregularis Mostler

Plate 2, fig. 5

1967 *Astropentagnathus irregularis* Mostler: 298–300, pl. 1, figs 1–11.

MATERIAL. 1 specimen: figured (X.596).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The blade occupies half the length of the unit and bears in excess of eight tall, erect denticles, subcircular in cross-section. The blade continues over the curved, platform-like posterior process as a row of nine low nodes. The posterior tip is sharp. On the inner side is a pointed, unornamented lateral process, directed anteriorly at an angle of 50° with the blade. A low, wide trough joins the blade and the process at the anterior end. On the outer side a bifurcating lateral process is situated opposite the inner lateral process, but is broken on this specimen. The process comprises two lobes, each ornamented by a row of nodes and expanded to form a platform. The entire aboral surface of the unit is deeply excavated.

REMARKS. The arrangement of the processes in *Astropentagnathus* is reminiscent of the genus *Amorphognathus*. Mostler (1967 : 299, 300) discussed the relationship between these two genera and stressed the fact that in *Astropentagnathus* the lateral processes are situated opposite one another, whereas in *Amorphognathus* the processes are offset.

Genus ***AULACOGNATHUS*** Mostler, 1967

TYPE SPECIES. *Aulacognathus kuehni* Mostler, 1967.

Aulacognathus kuehni Mostler

Plate 2, fig. 6

?1965 *Apsidognathus tuberculata* Walliser; Brooks & Druce: 375, pl. 12, figs. 1, 9, 10.
1967 *Aulacognathus kuehni* Mostler: 301, pl. 1, figs 12–15, 21, 24, 25.

MATERIAL. 17 specimens: figured (X.595).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The short free blade continues over the platform as a prominent nodose carina, becoming less pronounced towards the posterior end where it is deflected inwards at an angle of up to 50°. The inner side of the platform is characterized by a straight lateral process, directed anteriorly and bearing a prominent row of nodes, which forms an angle of approximately 45° with the carina. This process is ornamented by low nodes on the posterior side, but between the ridge and the carina on the anterior side is a deep, unornamented portion. The outer side of the platform is characterized by a tri-lobed process, which is separated from the carina by a trough which deepens anteriorly and posteriorly. The anteriorly and posteriorly directed lobes of the outer lateral process bear prominent rows of nodes, which are joined to form a ridge, curved convex to the carina. The central lobe is ornamented by tubercles. The expanded, inwardly deflected posterior process is also tuberculate. The aboral surface is deeply excavated and commonly contains basal material.

REMARKS. These specimens resemble in most characteristics those illustrated by Mostler (1967), but show a more marked inward deflection and expansion of the posterior end of the carina.

A morphological similarity to *Apsidognathus* is apparent in the tuberculate ornamentation of the oral surface. The broken specimens illustrated by Brooks & Druce (1965) as *Apsidognathus tuberculata* are probably referable to *Aulacognathus kuehni*.

Genus ***CARNIODUS*** Walliser, 1964

TYPE SPECIES. *Carniodus carnulus* Walliser, 1964.

Carniodus carinthiacus Walliser

Plate 5, figs 8–10

1964 ?*Carniodus carinthiacus* Walliser: 31, pl. 6, fig. 8; pl. 27, figs 20–26; text-fig. 4n.
1966 *Carniodus carinthiacus* Walliser; Spasov & Filipović: 38, pl. 1, fig. 3.
1966 *Carniodus carinthiacus* Walliser; Spasov: pl. 1, fig. 3.
1968 *Carniodus carinthiacus* Walliser; Nicoll & Rexroad: 24, pl. 5, figs 1, 2.
1969 ?*Carniodus carinthiacus* Walliser; Schönlaub: pl. 1, fig. 12.
1969 *Carniodus*? *carinthiacus* Walliser; Drygant: 54, pl. 1, fig. 5.

MATERIAL. 105 specimens: figured, S.2.64, S.2.65, (X.610).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The arched and bowed blade is thickened laterally to form a prominent marginal lip below the denticle row. The cusp is usually small and may be difficult to differentiate from the other high, central denticles of the blade. The denticles on both the anterior and posterior parts of the blade are strongly posteriorly inclined, laterally compressed and fused nearly to the tip. Each part of the blade bears up to nine denticles. The anterior part of the blade is commonly longer than the posterior. The basal groove is widest beneath the cusp and may contain basal material.

REMARKS. The specimens from this study show a greater range of variation than displayed by those illustrated by Walliser (1964). Forms with a long posterior extension of the blade, similar to those described by Nicoll & Rexroad (1968 : 25), are present. In some specimens the cusp is comparatively well developed and a closer similarity to other species of the genus is achieved.

A single specimen from the early Wenlock (Ticklerton 3) bears a small, posteriorly inclined aberrant branch, supporting two small denticles. The branch is situated on the outer side of the unit, beneath the denticle immediately posterior to the cusp.

Carniodus carnicus Walliser

Plate 5, fig. 11

1964 *Carniodus carnicus* Walliser: 32, pl. 6, fig. 11; pl. 28, figs 8–11.
1966 *Carniodus carnicus* Walliser; Spasov & Filipović: 38, pl. 1, fig. 16.
1968 *Carniodus carnicus* Walliser; Nicoll & Rexroad: 25, pl. 5, fig. 3.
1969 *Carniodus carnulus* Walliser; Schönlaub: pl. 1, fig. 5.

MATERIAL. 15 specimens: figured (X.611).

OCCURRENCE. Telychian (C_6) and early Wenlock.

Description. The unit is almost symmetrical and consists of a large, laterally compressed cusp, which is flanked on each side by three to six small, laterally compressed denticles. The size of the denticles and the height of the blade decrease away from the cusp, resulting in a marked tapering of the unit. The basal cavity is slightly flared beneath the cusp and continues as a groove to the ends of the blade.

Carniodus carnulus Walliser

Plate 5, figs 12–14

1964 *Carniodus carnulus* Walliser: 32, pl. 6, fig. 10; pl. 10, figs 20, 21; pl. 27, figs 27–38; pl. 28, fig. 1; text-fig. 4 a–f.
1966 *Carniodus carnulus* Walliser; Spasov & Filipović: 39, pl. 1, fig. 15.
1968 *Carniodus carnulus* Walliser; Nicoll & Rexroad: 25, pl. 5, figs 4, 5.

Material. 132 specimens: figured (X.612), (X.613), (X.614).

Occurrence. Telychian (C_5) to early Wenlock.

Description. The unit is slightly arched and more or less symmetrical with a tall, erect, central cusp. The anterior and posterior limbs of the blade are short and bear from two to six small, closely packed denticles, which decrease in size away from the cusp. The cusp and the denticles are laterally compressed. Beneath the denticle row the blade is commonly somewhat laterally expanded, whence it narrows towards the base. The basal cavity is slightly expanded below the cusp and extends as a shallow groove to the tips of the blade.

Aberrant forms bearing a denticulate lateral branch are common (Pl. 5, fig. 14). The branch usually arises from the posterior edge of the cusp, but may be situated on the anterior portion of the blade. A single aberrant specimen from the early Wenlock displays branches on both sides of the unit.

Carniodus carnus Walliser

Plate 5, figs 15, 16

1964 *Carniodus carnus* Walliser: 34, pl. 5, fig. 3; pl. 10, fig. 13; pl. 28, figs 2–7; text-fig. 4 y–z.
1966 *Carniodus carnus* Walliser; Spasov & Filipović: 40, pl. 1, figs 12, 13.
1968 *Carniodus carnus* Walliser; Nicoll & Rexroad: 26, pl. 5, figs 6–8.

Material. 99 specimens: figured, (X.615), S.2.72.

Occurrence. Telychian (C_5) to early Wenlock.

Description. The unit is asymmetrical with a tall cusp that may be erect or slightly curved posteriorly. The posterior limb of the blade is straight and bears from three to eleven short, closely packed denticles. A single, somewhat larger denticle may be present near the midlength of the limb. The anterior limb of the blade is directed downwards, bowed inwards and bears three to six small denticles. The denticle nearest the cusp is often considerably taller than the rest. The basal cavity is widest under the cusp and continues as a groove beneath the limbs of the blade, widening on the posterior limb beneath the single large denticle, when present.

REMARKS. The wide variation, remarked upon by Walliser (1964), in the angle between the limbs of the blade, the curve of the anterior limb and the dentition is apparent in this material.

The presence of a larger denticle on the posterior limb of some specimens was interpreted by Walliser (1964 : 17) as a fusion of the conodont of the species *Carniodus carnus* with one of the species *C. carnulus*, indicating association of the two forms in a single natural species. This type of fusion with *C. carnulus* is also displayed by some specimens of *Exochognathus latialatus* and *Neoprioniodus subcarnus*.

Carniodus spp.

Plate 5, figs 18, 19

Eighteen specimens referable to the genus *Carniodus* were recovered from Idwian and Fronian strata. Many specimens are too poorly preserved for specific identification, but a few resemble those illustrated by Walliser (1964 : pl. 4, fig. 12; pl. 29, figs 1–4) as *Carniodus* sp. In 11 of the specimens the anterior limb of the blade is directed downwards and bowed inwards, and these are referred to *Carniodus* cf. *C. carnus* Walliser (Pl. 5, fig. 18). A single specimen is referred to *Carniodus* cf. *C. eocarnicus* Walliser (Pl. 5, fig. 19).

Genus ***DIADELOGNATHUS*** Nicoll & Rexroad, 1968

TYPE SPECIES. *Diadelognathus excertus* Nicoll & Rexroad, 1968.

Diadelognathus nicolli sp. nov.

Plate 8, figs 2, 3

1968 *Diadeolognathus* n. sp. A. Nicoll & Rexroad: 30, pl. 6, figs 9, 10.

DERIVATION OF NAME. After R. S. Nicoll, one of the authors who originally described this species.

DIAGNOSIS. *Diadelognathus* Nicoll & Rexroad with a well-developed anterior process and an almost equally well-developed outer lateral process.

HOLOTYPE. Specimen (X.583).

MATERIAL. 11 specimens: figured (X.583), (X.584).

TYPE LOCALITY AND HORIZON. Wenlock Shales, Ticklerton, Shropshire. Sample Ticklerton 1.

OCCURRENCE. Early Wenlock.

DESCRIPTION. The posteriorly inclined cusp is expanded posteriorly at the base.

The transverse section of the cusp is a laterally compressed ellipse. The inner anterior margin of the cusp gives rise to a straight anterior process, which supports three to seven widely-spaced denticles. The denticles are elliptical in transverse section, inclined posteriorly and they decrease in size anteriorly. The anterior process narrows towards the tip. The outer lateral process arises from the outer anterior margin of the cusp and is directed perpendicularly outwards. The straight process bears two to four discrete, posteriorly curved denticles, subcircular in cross section. The aboral surface of the cusp is excavated by a very shallow cavity which continues as grooves under the processes.

Remarks. Nicoll & Rexroad (1968 : 27–28) described a phylogenetic sequence from *Diadelognathus primus*. through *D. excertus* to *D. nicolli*. Insufficient material has been recovered from the Welsh Borderland for this sequence to be recognized, but those specimens of *D. nicolli* with less well-developed lateral processes indicate a transition towards *D. excertus*. *D. excertus* itself has not, as yet, been recognized in Britain.

Diadelognathus primus Nicoll & Rexroad

Plate 8, fig. 1

1968 *Diadelognathus primus* Nicoll & Rexroad: 29, pl. 6, figs 7, 8.

Material. 1 specimen: figured (X.729).

Occurrence. C_{3-4}.

Description. The stout cusp is strongly curved posteriorly and is subcircular in transverse section. The base of the cusp is expanded and gives rise to two short processes, one directed outwards and the other directed inwards and anteriorly. Each process bears two very small denticles, those nearer the cusp being the larger. The entire aboral surface is occupied by a shallow cavity.

Genus ***DISTACODUS*** Hinde, 1879

Type species. *Machairodus incurvus* Pander, 1856.

Distacodus obliquicostatus Branson & Mehl

Plate 9, fig. 4

1933 *Distacodus obliquicostatus* Branson & Mehl: 41, pl. 3, fig. 2.
1964 *Acontiodus procerus* (Ethington) Serpagli & Greco: 198, pl. 37, figs 5, 6.
1968 *Distacodus obliquicostatus* Branson & Mehl; Nicoll & Rexroad: 31, pl. 7, figs 1–4.

Material. 1 specimen: figured (X.711).

Occurrence. Fronian.

Description. The apical portion of this specimen is missing, so the degree of curvature of the cone cannot be determined. The basal part of the unit is strongly laterally compressed and triangular in shape. The anterior and posterior edges are sharp. Each lateral face bears a medial costa that does not extend to the base. The entire base is excavated and the cavity is deep.

Genus ***DISTOMODUS*** Branson & Branson, 1947

Type species. *Distomodus kentuckyensis* Branson & Branson, 1947.

Distomodus? egregius (Walliser)

Plate 6, figs 3, 4, 9

1964 *Ligondina egregia* Walliser: 40, pl. 6, fig. 5; pl. 32, figs 3, 4.
1968 *Distomodus? egregia* (Walliser) Nicoll & Rexroad: 33, pl. 5, figs 26–28.

Material. 46 specimens: figured (X.641), (X.642), (X.643).

Occurrence. Fronian to early Wenlock.

Description. The long, stout cusp is curved posteriorly and in transverse section is biconvex, the outer side usually being more strongly convex than the inner. The inner anterior margin of the cusp bears a costa, which extends downwards to form a denticulate anticusp. The straight posterior bar is inclined downwards and bears several laterally compressed denticles, which are sometimes partially fused. A rounded or sharp lip, directed downwards and slightly posteriorly, is present at the base of the cusp on the outer side. In a very few specimens the lip bears a ridge, which continues onto the posterior edge of the cusp. A conical cavity beneath the cusp continues as a groove under the posterior bar and usually contains basal material.

Distomodus? extrorsus (Rexroad)

Plate 6, fig. 2

1964 *Neoprioniodus?* cf. *brevirameus* Walliser: pl. 29, fig. 11.
1967 *Ligondina? extrorsa* Rexroad: 36, pl. 2, figs 9, 10, 15–17.
1968 *Distomodus? extrorsus* (Rexroad) Nicoll & Rexroad: 34, pl. 5, fig. 23.

Material. 36 specimens: figured (X.640).

Occurrence. Idwian to Telychian.

Description. The long, stout cusp is curved posteriorly. The anterior and posterior edges are sharp, the outer lateral face is convex and the inner lateral face is flat or gently convex. The inner anterior margin is extended downwards into a short anticusp that may not be denticulate. The posterior bar is short and may only be a slight extension of the posterior margin of the cusp. The small denticles of the posterior bar are subcircular in transverse section. The cusp is excavated by a conical cavity, which extends beneath the posterior bar.

Remarks. Nicoll & Rexroad (1968 : 34) noted that *D.*? *extrorsus* evolved into *D.*? *egregius* by the development of a lip-like projection on the outer side and an increase in the denticulation of the anticusp. This lineage is also apparent in the Welsh Borderland, where *D.*? *extrorsus* first appears in older strata than *D.*? *egregius*.

Distomodus kentuckyensis Branson & Branson

Plate 6, figs 5–8, 11

1947 *Distomodus kentuckyensis* Branson & Branson: 553, pl. 81, figs 21–23, 27, 29–33, 36–41.
1967 *Distomodus kentuckyensis* Branson & Branson; Rexroad: 28, pl. 2, figs 11–14.
1968 *Distomodus kentuckyensis* Branson & Branson; Nicoll & Rexroad: 34, pl. 5, figs 24, 25.
1970 *Distomodus kentuckyensis* Branson & Branson; Pollock, Rexroad & Nicoll: 750, pl. 112, figs 7, 8.

Material. 125 specimens: figured (X.644), (X.645), (X.646), (X.647), (X.648).

Occurrence. Idwian to early Wenlock.

Description. The very large cusp is curved slightly posteriorly and inwards. The transverse section of the cusp is biconvex, the convexity of the inner face increasing markedly near the base. The anterior and posterior edges of the cusp are sharp. The anterior edge is extended downwards to form an anticusp, which in a few specimens bears fused denticles. The posterior bar, when present, is usually short and bears laterally compressed denticles that are commonly fused. The base of the cusp is deeply excavated and the cavity continues as a groove under the posterior bar.

Remarks. The range of variation of this species is very wide, especially in the development and dentition of the posterior bar and the anticusp. A few specimens have discrete denticles on the posterior bar. A single, poorly preserved specimen possesses a long posterior bar that bears nine closely packed denticles.

Distomodus triangularis tenuirameus (Walliser)

Plate 6, fig. 13.

1964 *Neoprioniodus triangularis tenuirameus* Walliser: 53, pl. 4, fig. 15; pl. 28, figs 21–24; text-fig. 6 a–c.
1968 *Neoprioniodus triangularis tenuirameus* Walliser; Igo & Koike: 13, pl. 3, figs 18, 19.
1970 *Distomodus* cf. *Neoprioniodus triangularis tenuirameus* Walliser; Pollock, Rexroad & Nicoll: 751, pl. 112, fig. 1.

Material. 14 specimens: figured (X.650).

Occurrence. Fronian and Telychian.

Description. The cusp is stout with sharp anterior and posterior edges. The inner lateral face is more strongly convex than the outer and may bear a blunt medial costa. The anterior margin may be very slightly extended to form a rudimentary anticusp. A short posterior bar bearing one or two poorly developed denticles may or may not be present. The moderately deep basal cavity occupies the entire aboral surface.

Remarks. Walliser (1964) separated his subspecies of *N. triangularis* by morphological differences and by differences in stratigraphic range. In the Welsh Borderland, however, the ranges of the two subspecies overlap. The distinction between the two subspecies may not be valid, but they are not, at present, considered synonymous, as clear evidence of morphological transition has not been found.

Distomodus triangularis triangularis (Walliser)

Plate 6, fig. 12.

1964 *Neoprioniodus triangularis triangularis* Walliser: 52, pl. 6, fig. 13; pl. 28, figs 25–30; text-fig. 6 d–f.
1966 *Neoprioniodus triangularis triangularis* Walliser; Spasov & Filipović: 43, pl. 2, fig. 4.
1968 *Neoprioniodus triangularis* Walliser; Nicoll & Rexroad: 42, pl. 5, fig. 17.
1970 *Distomodus triangularis triangularis* (Walliser) Pollock, Rexroad & Nicoll: 750, pl. 112, figs 2–6.

Material. 90 specimens: figured (X.651).

Occurrence. Idwian to early Wenlock.

Description. The cusp is stout, with sharp anterior and posterior edges. The outer side of the cusp is gently convex, the inner side bears a sharp ridge, which is extended laterally as a deep costa near the base. The antero-lateral and postero-lateral faces are concave. The anterior margin is extended downwards to form an anticusp, which is not denticulate. The posterior bar is directed downwards and bears from two to eight small, sharp denticles. The aboral surface is moderately deeply excavated beneath the cusp and is grooved beneath the anticusp and the posterior bar.

Distomodus sp. nov.

Plate 6, fig. 10

Material. 3 specimens: figured, S.3.30.

Occurrence. C_{3-4}.

Description. The cusp is tall, laterally compressed and slightly curved posteriorly. The anterior and posterior edges of the cusp are sharp, the lateral faces gently convex. The inner lateral face increases in convexity towards the base, where it flares inwardly and a little posteriorly. The anterior margin is extended downwards to form an anticusp, which bears three or four small, laterally compressed, partially fused denticles. The base of the cusp is excavated by a fairly shallow conical cavity, which terminates at a point near the anterior margin. The cavity continues as a narrow groove below the anticusp, and may be filled with basal material.

REMARKS. This species differs from other species of *Distomodus* in the possession of a denticulate anticusp combined with the absence of a posterior bar. There are too few specimens to warrant the erection of a specific name.

Genus ***DREPANODUS*** Pander, 1856

TYPE SPECIES. *Drepanodus arcuatus* Pander, 1856.

Drepanodus aduncus Nicoll & Rexroad

Plate 9, fig. 17

1968 *Drepanodus aduncus* Nicoll & Rexroad: 35, pl. 7, figs 11–15.

MATERIAL. 17 specimens: figured (X.715).

OCCURRENCE. Telychian and early Wenlock.

DESCRIPTION. The small cone is bent markedly inwards along its length. The anterior and posterior edges are sharp. The anterior margin is laterally compressed near the base and is extended to form a small, flat anticusp, which is inwardly flexed. Both lateral faces are convex, the unit flaring towards the base. The basal cavity is circular under the posterior portion of the unit and continues as a groove to the anterior tip. The cavity extends for less than half the length of the cone.

Drepanodus suberectus (Branson & Mehl)

Plate 9, fig. 16

1933 *Oistodus suberectus* Branson & Mehl: 111, pl. 9, fig. 7.
1935 *Oistodus suberectus* Branson & Mehl; Stauffer: 147, pl. 12, figs 14, 19, 28, 31, 35.
1951 *Oistodus suberectus* Branson & Mehl; Branson, Mehl & Branson: 8, pl. 2, figs 1–4.
1953 *Oistodus suberectus* Branson & Mehl; Rhodes: 229, pl. 21, figs 93, 94.
1954 *Drepanodus suberectus* (Branson & Mehl) Lindström: 568, pl. 2, figs 21, 22.
1955 *Drepanodus suberectus* (Branson & Mehl); Sannemann: 27, pl. 1, fig. 22, pl. 2, fig. 1.
1957 *Oistodus suberectus* Branson & Mehl; Glenister: 726, pl. 86, figs 12, 14.
1959 *Drepanodus suberectus* (Branson & Mehl); Ethington: 276, pl. 39, fig. 17.
1959 *Drepanodus suberectus* (Branson & Mehl); Stone & Furnish: 222, pl. 31, fig. 7.
1959 *Drepanodus suberectus* (Branson & Mehl); Sweet *et al.*: 1049, pl. 130, fig. 4.
1960 *Drepanodus suberectus* (Branson & Mehl); Pulse & Sweet: 253, pl. 35, figs 2, 7.
1960 *Drepanodus suberectus* (Branson & Mehl); Carlson: pl. 2, fig. 10.
1961 *Drepanodus suberectus* (Branson & Mehl); Bergström: 41, pl. 5, fig. 7, text-figs 3K, 4B.
1961 *Drepanodus suberectus* (Branson & Mehl); Wolska: 349, pl. 1, figs 8a, b.
1962 *Drepanodus suberectus* (Branson & Mehl); Sweet & Bergström: 1226, pl. 169, fig. 8.
1964 *Drepanodus suberectus* (Branson & Mehl); Ethington & Clark: 689, pl. 113, fig. 18.
1965 *Drepanodus suberectus* (Branson & Mehl); Barnett: 70, pl. 1, fig. 29; pl. 2, fig. 22.
1965 *Drepanodus suberectus* (Branson & Mehl); Merrill: 376, pl. 1, fig. 8.
1966 *Drepanodus suberectus* (Branson & Mehl); Winder: pl. 9, fig. 6.
1966 *Drepanodus suberectus* (Branson & Mehl); Oberg: 137, pl. 16, fig. 1.
1966 *Drepanodus suberectus* (Branson & Mehl); Webers (*partim*): 29, pl. 6, fig. 9 only.

1966 *Drepanodus suberectus* (Branson & Mehl); Hamar: 58 pl. 1 figs 8, 9.
1966 *Drepanodus suberectus* (Branson & Mehl); Schopf: 54 pl. 5 fig. 25.
1966 *Drepanodus suberectus* (Branson & Mehl); Bergström & Sweet: 330 pl. 35 figs 22, 23.
1966 *Drepanodus suberectus* (Branson & Mehl); Fahraeus: 23, pl. 2, fig. 10, text-fig. 20.
1967 *Drepanodus suberectus* (Branson & Mehl); Rexroad: 30, pl. 2, fig. 4.
1970 *Drepanodus suberectus* (Branson & Mehl); Pollock, Rexroad & Nicoll: 751, pl. 114, fig. 21.

MATERIAL. 41 specimens: figured (X.714).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The symmetrical cone is slightly inclined or curved posteriorly and is somewhat laterally compressed. The anterior and posterior edges are sharp, the lateral faces are convex. The base is flared in all directions to produce a subcircular or oval outline. A shallow, conical cavity is excavated on the aboral surface.

Drepanodus spp.

Plate 9, figs 14, 15

Eighteen specimens representing various species of *Drepanodus* are present in the collections. Some of the specimens may be indigenous, others are probably not. In particular, eight specimens from the Pentamerus Beds of Ticklerton Brook are associated with other species that appear to be derived from Ordovician strata. Since the number of specimens is small and their stratigraphic value negligible, they have not been compared closely with described species of *Drepanodus*, but some of the forms recovered are illustrated.

Genus ***EXOCHOGNATHUS*** Pollock, Rexroad & Nicoll, 1970

TYPE SPECIES. *Trichonodella brassfieldensis* Branson & Branson, 1947.

Exochognathus brassfieldensis (Branson & Branson)

Plate 7, fig. 4

1947 *Trichonodella brassfiedensis* Branson & Branson (*partim*): 551, pl. 81, fig. 12 only; pl. 82, fig. 47 only.
1967 *Trichonodella brassfieldensis* Branson & Branson; Rexroad: 56, pl. 3, figs 27, 28.
1968 *Trichonodella brassfieldensis* Branson & Branson; Nicoll & Rexroad: 62, pl. 5, figs 13, 14.
1970 *Exochognathus brassfieldensis* (Branson & Branson) Pollock, Rexroad & Nicoll: 753, pl. 112, fig. 24.

MATERIAL. 59 specimens; figured (X.665).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The asymmetrical unit consists of a stout cusp, two lateral processes and a posterior bar. The posteriorly curved cusp bears three prominent costae, which merge downwards with the processes. The outer lateral process, which is shorter and is directed more sharply downwards than the inner lateral process, bears three or four compressed denticles, which may be completely fused.

In a few specimens the outer lateral process is not denticulate. The inner lateral process points downwards and inwards, and bears up to six discrete or fused denticles. The posterior bar is short and may not be denticulate, although up to five denticles are usually present. The cavity is deep beneath the cusp and extends almost to the tips of the processes.

Exochognathus brevialatus (Walliser)

Plate 7, figs 8, 9

1964 *Roundya brevialata* Walliser: 69, pl. 4, fig. 16; pl. 31, figs 8–10.
1964 *Roundya truncialata* Walliser: 72, pl. 4, fig. 7; pl. 31, figs 3–6.
1970 *Exochognathus brevialatus* (Walliser) Pollock, Rexroad & Nicoll: 753, pl. 112, figs 29, 30.

MATERIAL. 46 specimens: figured (X.668), (X.669).

OCCURRENCE. Idwian to early Wenlock. Most abundant in the Idwian.

DESCRIPTION. The curved cusp supports two lateral processes and a posterior bar, all of which are directed downwards. Three costae extend along the cusp in line with the processes. The lateral processes together form a steep, symmetrical or slightly asymmetrical arch, and display considerable variation in length and denticulation. The denticulate posterior bar is inclined downwards and is sometimes directed slightly laterally, causing asymmetry of the unit. The cavity is small under the cusp and extends for a short distance beneath the processes.

REMARKS. The species *Roundya truncialata* of Walliser (1964) included forms with long lateral processes, bearing several denticles. Walliser considered that *R. brevialata* evolved from *R. truncialata* by a decrease in the length and dentition of the lateral processes. Pollock, Rexroad & Nicoll (1970 : 753) recorded numerous specimens intermediate between the two extremes and considered they were conspecific. In the Welsh Borderland collections, specimens of the '*truncialata*-type' are common in the Idwian and can be readily distinguished from those of the '*brevialata*-type' that occur in small numbers in younger strata. It is possible that two chronological subspecies could be defined, but there is inadequate material for an attempt to be made here.

Exochognathus caudatus (Walliser)

Plate 7, fig. 13

1964 *Roundya caudata* Walliser: 70, pl. 5, fig. 9; pl. 31, figs 18, 19.
1967 *Roundya caudata* Walliser; Rexroad: 58, pl. 3, figs 29, 30.
1970 *Exochognathus caudatus* (Walliser) Pollock, Rexroad & Nicoll: 753, pl. 112, figs 31–33.

MATERIAL. 62 specimens: figured (X.674).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The slightly twisted, curved cusp bears three costae that give rise to two lateral processes and a posterior bar. The lateral processes point sharply downwards and together form an arch, which is more or less symmetrical Both lateral process bear discrete denticles. The posterior bar is inclined downwards and is commonly very long, bearing discrete, laterally compressed denticles. The cusp is deeply excavated and the cavity continues as a groove beneath the processes.

REMARKS. There is a close relationship between *E. caudatus* and *E. detortus*, the latter possessing a more strongly twisted cusp and more strongly asymmetrical lateral processes. Both species are probably descended from *E. brassfieldensis*. Specimens showing morphological transition between the three species occur frequently in the collections.

Exochognathus detortus (Walliser)

Plate 7, figs 7, 12

1964 *Roundya detorta* Walliser: 70, pl. 5, fig. 8; pl. 31, figs 15–17.
1968 *Roundya detorta* Walliser; Nicoll & Rexroad: 58, pl. 6, figs 16–18.

MATERIAL. 36 specimens: figured (X.672), (X.673).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is curved posteriorly and strongly twisted. Three costae on the cusp give rise to two lateral processes and a posterior bar. The lateral processes bear discrete denticles and together form an asymmetrical arch. The posterior bar is commonly directed horizontally and is of similar length to the lateral processes. The laterally compressed denticles of the posterior bar may be discrete or fused. The cusp is deeply excavated and the cavity extends as a groove beneath the processes.

Exochognathus keislognathoides Pollock, Rexroad & Nicoll

Plate 7, fig. 5

1967 *Keislognathus*? n. sp. Rexroad: 59, pl. 3, figs 20, 21.
1970 *Exochognathus keislognathoides* Pollock, Rexroad & Nicoll: 753, pl. 112, figs 25–28.

MATERIAL. 19 specimens: figured (X.666).

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. The curved cusp is approximately triangular in transverse section and bears a costa at each edge. The inner antero-lateral process is a long, slender, non-denticulate anticusp, bearing a continuation of the inner anterior costa of the cusp. The outer lateral process is inclined outwards and downwards, and bears discrete denticles. The posterior bar is inclined slightly downwards and also bears discrete denticles. The cavity is deep beneath the cusp and continues as a deep groove beneath the processes.

Exochognathus latialatus (Walliser)

Plate 7, figs 10, 11

1964 *Roundya latialata* Walliser: 71, pl. 6, fig. 15; pl. 31, figs 11–14.

MATERIAL. 28 specimens: figured (X.670), (X.671).

OCCURRENCE. Telychian (C_6).

DESCRIPTION. The curved cusp is almost square in transverse section and supports two lateral processes and a posterior bar. The lateral processes are deep, more or less symmetrical and bear several closely-packed denticles. The long posterior bar is directed slightly downwards and bears several small, appressed denticles. A larger denticle may be present near the midlength of the bar. The cavity is deep beneath the cusp and continues as a groove under the processes, widening beneath the larger denticle on the posterior bar.

REMARKS. Some specimens show the probable fusion of *E. latialatus* and *Carniodus carnulus*. A similar development is noted in some specimens of *Carniodus carnus* and *Neoprioniodus subcarnus*.

Exochognathus sp. nov.

Plate 7, fig. 6

1967 *Rhynchognathodus*? n. sp. Rexroad: 60, pl. 3, fig. 23.

MATERIAL. 1 specimen: figured (X.667).

OCCURRENCE. Fronian.

DESCRIPTION. Near the apex of the unit the cusp is posteriorly curved. The anterior face is gently convex, with sharp lateral edges. The posterior edge is sharp. One lateral face is broader than the other. The cusp flares towards the base and the lateral edges on the proximal portion bear small, sharp denticles, fused nearly to their apices. The posterior margin of the proximal portion is broken on the only specimen available for study. The entire base of the unit is deeply excavated.

REMARKS. This specimen appears to belong to the same species as those described by Rexroad (1967) as *Rhynchognathodus*? n. sp. Pollock, Rexroad & Nicoll (1970 : 752) include this species in their list of those referable to the genus *Exochognathus*. It is considered inadvisable to erect a specific name for the species herein on the basis of a single specimen.

Rexroad (1967) described the denticulate margins of his specimens as extending slightly beyond the lamellae of the flared base as lateral processes. This feature is not apparent on the specimen described above.

Genus ***GOTHODUS*** Lindström, 1954

TYPE SPECIES. *Gothodus costulatus* Lindström, 1954.

***Gothodus*? sp. nov.**

Plate 6, fig. 1

MATERIAL. 4 specimens: figured (X.649).

OCCURRENCE. Idwian and Fronian.

DESCRIPTION. The slender cusp is sharply recurved at about midlength. One lateral face of the cusp is flat or very gently convex, the other is strongly convex and bears a poorly developed costa, which may only be apparent towards the base. The anterior and posterior edges of the cusp are sharp. The cusp supports three processes, one lateral, one anterior and one posterior. The anterior process is a short undenticulated anticusp, in direct continuation with the anterior margin of the cusp. The posterior margin of the cusp gives rise to the posterior process, which is short, directed downwards and bears one or two discrete, rounded denticles. The lateral process is a short downward continuation of the lateral costa and bears one or two small denticles. The basal cavity is deep and conical, terminating in a point near the anterior edge, close to the point of recurvature of the cusp.

REMARKS. Lindström (1954 : 569) defined *Gothodus* as follows: 'The genus *Gothodus* realizes the combination three processes or definite costae, two of which are undenticulated. The third costa runs into the denticulated oral margin.' The specimens described above depart from this definition in that only one process is undenticulated. The generic assignment of the species is therefore questioned. This species also differs from the previously described species of *Gothodus*, *G. costulatus* Lindström (1954 : 569, pl. 5, figs 23–25) and *G. communis* Ethington & Clark (1964 : 690, pl. 114, figs 6, 14), in possessing only a short, poorly denticulate posterior process. The arrangement of the processes and the characteristics of the basal cavity of the present specimens are morphologically consistent with an assignment to *Gothodus*.

Too few specimens have been recovered to warrant the erection of a specific name.

Genus ***HADROGNATHUS*** Walliser, 1964

TYPE SPECIES. *Hadrognathus staurognathoides* Walliser, 1964.

Hadrognathus staurognathoides Walliser

Plate 2, figs 8, 10, 11

1964 *Hadrognathus staurognathoides* Walliser: 35, pl. 5, fig. 2; pl. 13, figs 6–15.
1965 *Hadrognathus staurognathoides* Walliser; Brooks & Druce: 376, pl. 12, figs 5, 6.
1968 *Hadrognathus staurognathoides* Walliser; Nicoll & Rexroad: 36, pl. 3, figs 12–14.

MATERIAL. 70 specimens: figured (X.590), (X.591), (X.592).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The unit consists of an anterior process, a posterior process, an inner lateral process and a bifurcating outer lateral process. All the processes are expanded to give a platform. The anterior process is often longer than the others and commonly bears a central row of well-developed, tall denticles, which are discrete at the anterior end. The posterior process is curved inwardly. The ornamentation of the oral surface of the posterior and lateral processes varies from feebly nodose to extremely irregular. The less nodose forms possess a low central ridge along each process. The outline of each process may be lanceolate or expanded and lobate. In some specimens the anterior process is of similar length and morphology to the others and may be difficult to distinguish. The entire aboral surface is deeply excavated and is often filled with basal material.

Remarks. The wide range of variation of this species is apparent in this material. A single juvenile specimen is similar to that illustrated by Walliser (1964 : pl. 13, fig. 6) and is morphologically close to representatives of the genus *Amorphognathus*. A phylogenetic link between *Amorphognathus* and *Hadrognathus* is possible.

Genus ***HIBBARDELLA*** Ulrich & Bassler, 1926

Type species. *Prioniodus angulatus* Hinde, 1879.

Remarks. The type specimens of *Hibbardella* were restudied by Huddle (1968 : 12–15), who concluded that *Roundya* Hass was a junior synonym of *Hibbardella* Bassler. The diagnosis given by Huddle for *Hibbardella* was as follows: 'Conodonts consisting of a denticulate posterior bar, terminal cusp, and symmetrical anterior arch. Bars thick and round. Denticles discrete and rounded.' Those Llandovery species that have been referred to *Roundya*, but show a degree of asymmetry, were transferred to *Exochognathus* by Pollock, Rexroad & Nicoll (1970 : 751–753). Llandovery species that show no phylogenetic relationship to *Exochognathus* and possess a symmetrical anterior arch are herein included in *Hibbardella*.

Hibbardella? prima (Walliser)

Plate 6, fig. 16

1964 ?*Roundya prima* Walliser: 71, pl. 4, fig. 6; pl. 31, figs 1, 2.

Material. 2 specimens: figured (X.703).

Occurrence. Fronian (C_{1-2}).

Description. The cusp is posteriorly curved and bears three ridges, one on each antero-lateral margin and the third on the posterior face. The anterior face of the cusp is gently convex. The two antero-lateral ridges expand laterally near the base to form small, serrated processes. The ridge on the posterior face is extended into a denticulate posterior bar. The entire aboral surface is deeply excavated.

Remarks. The arrangement of the processes and the symmetry of the unit are consistent with a generic assignment to *Hibbardella*. The poor development and denticulation of the processes, however, render this assignment questionable.

Hibbardella? trichonodelloides (Walliser)

Plate 6, figs 17, 18

1964 ?*Roundya trichonodelloides* Walliser: 72, pl. 6, fig. 2; pl. 31, figs 22–25.

MATERIAL. 9 specimens: figured (X.704), (X.705).

OCCURRENCE. Telychian.

DESCRIPTION. The lateral processes are directed laterally and anteriorly and bear flat, closely-packed denticles. The cusp is curved posteriorly and is extended into a posterior bar at the base. The posterior bar may or may not bear a few irregular denticles. The basal cavity is deepest beneath the junction of the processes. The cavity extends as a narrow groove under the lateral processes and as a wide groove beneath the posterior bar.

REMARKS. There is a close relationship with *Trichonodella excavata*, the two species being linked by intermediate forms. Only those specimens with a clearly developed posterior bar are included in *H.? trichonodelloides*.

Hibbardella sp. nov.

Plate 6, figs 14, 15

MATERIAL. 3 specimens: figured (X.706), (X.707).

OCCURRENCE. C_{3-4}.

DESCRIPTION. The stout, posteriorly curved cusp is subcircular in transverse section. The anterior margin of the cusp gives rise to two lateral processes, directed laterally and downwards and together forming an almost symmetrical arch. Each lateral process bears three or four discrete denticles, which are subcircular in transverse section. The posterior bar is straight and bears discrete, posteriorly inclined denticles, the one nearest the cusp being the smallest. The aboral surface of the processes is occupied by a wide, shallow groove, which deepens slightly to form a shallow cavity beneath the cusp.

REMARKS. Too few specimens have been recovered to enable comment on the range of variation or the relationships of this species.

Genus ***HINDEODELLA*** Ulrich & Bassler, 1926

TYPE SPECIES. *Hindeodella subtilis* Ulrich & Bassler, 1926.

Hindeodella equidentata Rhodes

Plate 8, fig. 19

1953 *Hindeodella equidentata* Rhodes: 303, pl. 23, figs 248, 252–254.
1957 *Hindeodella equidentata* Rhodes; Walliser: 34, pl. 2, fig. 33.
1960 *Hindeodella equidentata* Rhodes; Ziegler: 182, pl. 15, fig. 10.
1960 *Hindeodella* cf. *H. equidentata* Rhodes; Walliser: 30, pl. 8, fig. 15.

1962 *Hindeodella equidentata* Rhodes; Ethington & Furnish: 1267, pl. 173, fig. 2.
1962 *Hindeodella equidentata* Rhodes; Spasov & Veselinović, 238 pl. 2, figs 10, 11.
1964 *Hindeodella equidentata* Rhodes; Walliser: 36, pl. 8, fig. 3; pl. 32, fig. 11.
1965 *Hindeodella equidentata* Rhodes; Philip: 102, pl. 8, fig. 11.
1966 *Hindeodella equidentata* Rhodes; Spasov & Filipović: 41, pl. 2, fig. 12.
1966 *Hindeodella equidentata* Rhodes; Philip: 445, pl. 3, fig. 1.
1969 *Hindeodella excavata* (Branson and Mehl) Jeppson (*partim*): 18, text-figs 1J, 3D.

MATERIAL 70 specimens: figured (X.695).

OCCURRENCE. Fronian to early Wenlock.

DESCRIPTION. The slender cusp is slightly posteriorly inclined. The anterior and posterior edges of the cusp are sharp. The posterior bar is long, deep, straight or a little curved, and bears several discrete, posteriorly inclined denticles. The denticle height decreases away from the cusp. The anterior bar is bent sharply inwards and bears five or more slender denticles. A basal groove underlies the entire unit and is slightly widened beneath the cusp.

Genus ***ICRIODELLA*** Rhodes, 1953

TYPE SPECIES. *Icriodella superba* Rhodes, 1953.

REMARKS. In recent publications the genus *Icriodella* has been orientated with the blade posterior and the platform anterior (Bergström & Sweet 1966; Schopf 1966; Pollock, Rexroad & Nicoll 1970). Pollock *et al.* (1970 : 754) pointed out that this orientation was necessitated by the slight inclination of the denticles of the blade away from the platform.

Icriodella deflecta sp. nov.

Plate 1, figs 4–7

1970 *Icriodella* n. sp. Pollock, Rexroad and Nicoll: 755, pl. 111, figs 20, 21.

DERIVATION OF NAME. With reference to the deflection of the platform inwards from the line of the blade.

DIAGNOSIS. *Icriodella* Rhodes with a blade and platform of approximately equal length. The platform is deflected out of line with the blade by about 45°.

HOLOTYPE. Specimen (X.561).

MATERIAL. 53 specimens: figured (X.561), S.1.2, (X.562), S.1.4.

TYPE LOCALITY AND HORIZON. The Venusbank Formation of Hope Quarry, sample H.Q.3.

OCCURRENCE. Late Idwian and early Fronian.

DESCRIPTION. The platform is narrow and bears two rows of nodes that are usually offset. The two rows may merge into a single row towards the anterior tip. The blade is of similar length to the platform and typically bears seven denticles fused nearly to the tips. The anterior denticle forms a small cusp, but is only slightly larger than the remainder. The platform is deflected by about 45° from the line of the blade. A strong lateral flange is present on the outer side of the unit at the junction of the blade and the platform. A ridge runs from the sharp tip of the flange to the cusp, and in mature forms may bear small denticles. A small, unornamented lateral flange is also present on the inner side, somewhat posterior of midlength. The entire aboral surface is excavated, the cavity being deepest beneath the centre of the unit.

REMARKS. *Icriodella deflecta* sp. nov. differs from *I. discreta*, from which it is probably descended, in the sharp angular deflection between the blade and platform, and in the greater number of denticles on the blade. It differs from the younger species, *I. inconstans* and *I. malvernensis*, in that the nodes of the platform are not laterally elongated.

Icriodella discreta Pollock, Rexroad & Nicoll

Plate 1, figs 1–3

1970 *Icriodella discreta* Pollock, Rexroad & Nicoll: 754, pl. 111, figs 27–30.

MATERIAL. 15 specimens: figured (X.585), (X.586), (X.587).

OCCURRENCE. Strata of probable early Idwian age.

DESCRIPTION. The platform bears two rows of nodes that are commonly laterally paired. The blade may be of similar length to the platform or a little shorter. The blade bears about four fused denticles, of which the anterior is conspicuously the largest and forms a prominent cusp. The platform is deflected by a few degrees from the line of the blade. An outer lateral flange is present at the junction of the blade and platform, and an inner lateral flange is situated posterior of the centre of the unit. The aboral surface is entirely excavated, the cavity being deepest beneath the cusp.

REMARKS. *Icriodella discreta* shows morphological similarities to the Ordovician species *I. superba* Rhodes, but a phylogenetic link has not, as yet, been demonstrated.

Icriodella inconstans sp. nov.

Plate 1, figs 13–17

DERIVATION OF NAME. Latin, variable.

DIAGNOSIS. *Icriodella* Rhodes with a straight platform bearing two parallel rows of nodes, which are laterally elongated, especially in the central portion. A well-developed cusp is situated at the anterior end of the blade and is flanked by a strong, unornamented lateral flange on the outer side and a poorly-developed flange on the inner side.

HOLOTYPE. Specimen (X.563).

Material. 356 specimens: figured (X.563), (X.564), S.1.9, (X.565), (X.566).

Type locality and horizon. The Wych Formation of Gullet Quarry, sample Gullet 2.

Occurrence. Telychian (C_5).

Description. The unit is narrow and elongated and consists of a posterior blade and an anterior platform. The tall, laterally compressed blade is straight or slightly curved and is shorter than the platform. The blade consists of five to eight fused denticles, the anterior being considerably larger than the remainder and forming a prominent cusp. The platform is straight and may be in direct continuation with the blade or deflected by an angle of up to 20°. In many specimens the blade and platform diverge from a common point, in others there is considerable lateral offset. The platform is low, lanceolate in oral view and bears two parallel rows of nodes, which are laterally elongated, particularly in the central portion. On the outer side of the unit a well-developed, pointed flange is situated immediately anterior to the cusp. The posterior edge of the flange bears a ridge which extends upwards onto the antero-lateral margin of the cusp. The anterior portion of the outer lateral flange is wide and unornamented. A less prominent lateral flange is situated below the cusp on the inner side of the unit. The entire aboral surface is excavated, the cavity being deepest beneath the area immediately anterior of the cusp. The cavity may contain basal material.

Remarks. This species differs from older species of *Icriodella* in the ornamentation of the platform and in the length and height of the blade. The small angle between the blade and platform also serves to distinguish *I. inconstans* sp. nov. from *I. deflecta* sp. nov. The straight platform and the absence of ornamentation on the outer lateral flange distinguishes the species from *I. malvernensis* sp. nov.

Icriodella malvernensis sp. nov.

Plate 1, figs 9–12

Derivation of name. After the Malvern Hills.

Diagnosis. *Icriodella* Rhodes with a blade and platform that are curved in opposing directions to give a sigmoidal shape in oral view. The outer lateral flange is very well developed and bears from one to three laterally elongated ridges.

Holotype. Specimen (X.567).

Material. 63 specimens: figured (X.567), (X.568), (X.569), (X.570).

Type locality and horizon. 'Sycamore Tree Quarry', West Malvern, sample West Malvern 1.

Occurrence. Telychian (probably C_5).

Description. The unit consists of a posterior blade and an anterior platform, which are curved in opposing directions to give a sigmoidal shape in oral view. The tall blade comprises five to eight laterally compressed, fused denticles, the anterior being the largest and forming a cusp. The platform bears two parallel rows of nodes, which are laterally elongated, especially somewhat posterior of the central portion. The angle between the line of the blade and the platform is between 20° and 40°. There may or may not be lateral offset between the blade and platform. The outer lateral flange is very strongly developed and at the posterior edge bears a ridge, which continues onto the antero-lateral margin of the cusp. The anterior portion of the flange is ornamented by one to three tall, laterally elongated ridges, which diverge from a point anterior to the cusp. A poorly developed, unornamented inner lateral flange is developed below the cusp on the inner side of the unit. The entire aboral surface is deeply excavated.

Remarks. The relationship between this species and *I. inconstans* sp. nov. is clearly apparent in the form of the blade and in the form and ornamentation of the platform. *I. malvernensis* is easily distinguished, however, by the curvature of the blade and platform and by the ornamentation of the outer lateral flange.

Specimens of *Icriodella malvernensis* appear to have been paired asymmetrically in the conodont-bearing organism. The asymmetry is apparent in the ornamentation of the outer lateral flange. Mature specimens of left forms display two or three well-developed ridges on the flange (Pl. 1, figs 9, 10, 12), whereas right forms possess one, or occasionally two, less well-developed nodose ridges (Pl. 1, fig. 11).

Two specimens from strata of C_{3-4} age are identified as *Icriodella* cf. *I. malvernensis* (Pl. 1, fig. 8). These appear to be transitional from *I. deflecta* sp. nov. to *I. malvernensis* sp. nov. and indicate a phylogenetic relationship between the two species. These intermediate forms show slight sigmoidal curvature, but the nodes on the platform are not laterally elongated. The outer lateral flange is ornamented by a single node.

Genus ***ICRIODINA*** Branson & Branson, 1947

Type species. *Icriodina irregularis* Branson & Branson, 1947.

Remarks. Representatives of the genus *Icriodina* are fragile and the original description (Branson & Branson 1947 : 550–551) was based on incomplete specimens. Rexroad (1967 : 32–33) recognized that complete specimens bear four processes and are cruciform in shape. No complete specimens were recovered in this study, but some examples have up to three of the processes intact.

Icriodina irregularis Branson & Branson

Plate 2, fig. 1

1947 *Icriodina irregularis* Branson & Branson: 551, pl. 81, figs 3–11, 18, 19.
1967 *Icriodina irregularis* Branson & Branson; Rexroad: 33, pl. 2, figs 18–21.
1968 *Icriodina irregularis* Branson & Branson; Nicoll & Rexroad: 37, pl. 3, figs 10, 11.

Material. *ca.* 12 specimens: figured (X.588).

Occurrence Idwian and early Fronian.

Description. The complete unit consists of four processes, situated approximately at right angles to one another to give a cruciform shape. In none of the specimens are all the processes intact. The anterior and posterior processes are commonly longer than the lateral processes. The oral surface is ornamented by irregular nodes, which often coalesce to form low ridges. In oral view, the outline of the individual processes is commonly lanceolate, but in some examples the tips are expanded and broad rather than pointed. The entire aboral surface is deeply excavated and may contain basal material.

Remarks. *Icriodina* appears to be closely related to *Icriodella*, and representatives of the two genera occur in association in the Welsh Borderland. The platform portion of mature specimens of *Icriodella* may show a similar lanceolate shape and nodose ornamentation to that of the processes of *Icriodina irregularis*, and broken specimens are sometimes difficult to differentiate. As remarked by Rexroad (1967 : 34) the broken specimens figured by Walliser (1964 : pl. 4, fig. 3; pl. 11, figs 10, 11) as *I. irregularis* are probably referable to *Icriodella*.

Estimation of the abundance of *I. irregularis* is complicated by the frequent occurrence of fragments for which positive identification is impossible. The figures given herein are based mainly upon specimens which display two or more ornamented processes and the true abundance of the species is probably a little greater.

Icriodina sp.

Plate 2, fig. 2

Material. 1 specimen: figured (X.589).

Occurrence. Late Fronian or early Telychian.

Description. The slightly damaged specimen consists of four processes of similar length, arranged approximately at right angles. Denticulation is preserved on only three of the processes, each of which bears a single row of erect denticles. On two opposing processes, the denticles are fused nearly to the tip, the longer process bearing eight denticles and the shorter five. The third denticulate process bears six free, slightly appressed denticles. Each process flares downwards from the base of the denticles. The aboral surface is very deeply excavated and the walls of the processes are consequently thin.

Remarks. This specimen is similar in many respects to *Icriodina stenolophata* Rexroad (1967 : 34–35, pl. 2, figs 22–24), which, however, shows distinct lateral processes that are 'no more than one-half the length of the longitudinal processes'. The possession of four processes of similar length causes this specimen to fall outside the known variation range of *I. stenolophata*.

Genus ***LIGONODINA*** Ulrich & Bassler, 1926

Type species. *Ligonodina pectinata* Ulrich & Bassler, 1926.

Ligonodina kentuckyensis Branson & Branson

Plate 8, figs 15, 16

1947 *Ligonodina kentuckyensis* Branson & Branson: 555, pl. 82, figs 28, 35.
1967 *Ligonodina kentuckyensis* Branson & Branson; Rexroad: 35, pl. 2, fig. 5.
1970 *Ligonodina kentuckyensis* Branson & Branson; Pollock, Rexroad & Nicoll: 755, pl. 114, figs 9, 10.

MATERIAL. 76 specimens: figured (X.696), (X.697).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The posteriorly curved cusp is subcircular to elliptical in transverse section. The inner lateral process is directed downwards and somewhat anteriorly, bearing four or five denticles. The posterior bar is straight or slightly curved and bears about six posteriorly inclined denticles. The two denticles nearest the cusp are commonly much smaller than the others. The basal cavity is widest beneath the cusp and is extended as a groove below the posterior bar.

REMARKS. In addition to specimens that are readily referable to *L. kentuckyensis*, there are several that show transition towards *L. salopia* and *L. silurica*. Ethington & Furnish (1962 : 1272) placed *L. silurica*, *L. kentuckyensis* and *L. salopia* in synonymy, but there appear to be valid morphological differences as well as differences in stratigraphic distribution. Several specimens that belong to this group of species are, however, difficult to refer with certainty to any single species, the situation being complicated by the fragmentary nature of much of the material.

Ligonodina petila Nicoll & Rexroad

Plate 8, fig. 11

1968 *Ligonodina petila* Nicoll & Rexroad: 38, pl. 5, figs 20–22.

MATERIAL. 10 specimens: figured (X.702).

OCCURRENCE. Late Fronian or early Telychian to early Wenlock.

DESCRIPTION. The cusp is curved slightly posteriorly and is subcircular to elliptical in transverse section. The inner lateral process is directed downwards and posteriorly, bearing four discrete denticles. The short posterior bar is straight and slender, supporting three or four widely spaced denticles, which are inclined a little posteriorly. The basal cavity is small and is not laterally expanded beneath the cusp.

Ligonodina salopia Rhodes

Plate 8, fig. 17

1953 *Ligonodina salopia* Rhodes: 307, pl. 23, figs 245, 257, 260.

MATERIAL. 19 specimens: figured (X.698).

OCCURRENCE: Idwian to early Wenlock.

DESCRIPTION. The cusp is stout and posteriorly curved. The transverse section of the cusp is subcircular to elliptical. The antero-lateral process is directed downwards, inwards and more or less anteriorly, and is not in direct continuation with the cusp. Five or six posteriorly inclined denticles are situated on the process. The posterior bar is straight and deep and bears discrete, posteriorly inclined denticles. The basal cavity is widest and deepest beneath the cusp and continues as a shallow groove beneath the processes.

Remarks. The specimens figured by Rhodes (1953) possess antero-lateral processes that are clearly isolated from the cusp. Only specimens that exhibit this feature have been included in *L. salopia* of this study. The specimens figured by Walliser (1964 : pl. 32, figs 5, 10) as *L. salopia* do not show this feature and Rexroad (1967 : 35) considered that they probably belonged in *L. kentuckyensis*. Specimens from this study which are morphologically similar to those of Walliser have been included in *L. kentuckyensis*.

Ligonodina silurica Branson & Mehl

Plate 8, figs 10, 13

1933 *Ligonodina silurica* Branson & Mehl: 48 pl. 3 figs 18–20.
1957 *Ligonodina ingens* Walliser: 37 pl. 2, fig. 20.
1957 *Ligonodina silurica* Branson & Mehl; Walliser: 38, pl. 2, fig. 10.
1964 *Ligonodina silurica* Branson & Mehl; Walliser: 42, pl. 8, fig. 13; pl. 2, fig. 10.
1969 *Ligonodina silurica* Branson & Mehl; Philip: 291, pl. 18, figs 18, 19, 23, 25.
1970 *Ligondina* cf. *L. silurica* Branson & Mehl; Pollock, Rexroad & Nicoll: 755, pl. 114, figs 7, 8.

Material. 36 specimens: figured (X.699), (X.700).

Occurrence. Fronian to early Wenlock.

Description. The stout, posteriorly curved cusp is subcircular in transverse section. The inner lateral process is essentially a downward extension of the inner anterior margin of the cusp and bears five to seven discrete, closely spaced denticles. The posterior bar is commonly curved in lateral view and bears closely packed denticles. The cavity is deepest and widest beneath the cusp and extends as a wide, shallow groove beneath the processes.

Remarks. The diagnostic feature of this species, as noted by Walliser (1964 : 42), is that a true antero-lateral branch does not exist, but the denticles are on the inner side of a long, downward continuation of the cusp.

Ligonodina? variabilis Nicoll & Rexroad

Plate 8, fig. 14

1964 *Hindeodella* n. sp. Walliser: 36, pl. 7, fig. 16; pl. 32, figs 25, 28, 30.
1968 *Ligonodina? variabilis* Nicoll & Rexroad: 39, pl. 4, figs 12–14.
1970 *Ligonodina? variabilis* Nicoll & Rexroad; Pollock, Rexroad & Nicoll: 755, pl. 114, figs 11, 12.

Material. 67 specimens: figured (X.701).

Occurrence. Fronian to early Wenlock.

Description. The cusp is posteriorly curved, often a little twisted, and is laterally compressed with sharp anterior and posterior margins. The antero-lateral process is bent inwards and, to a varying degree, downwards. The denticles of the process are two to five in number and are compressed in the plane of the process. The posterior bar is laterally compressed, straight or curved, and bears a large number of closely-packed, posteriorly inclined denticles. The small basal cavity is situated beneath the cusp and extends as a rapidly tapering groove beneath each process.

Remarks. This species is very variable and includes forms that approach *Hindeodella* and *Ligonodina* in morphology. The generic assignment is, therefore, questioned.

Genus ***LONCHODINA*** Ulrich & Bassler, 1926

Type species. *Lonchodina typicalis* Ulrich & Bassler, 1926.

Lonchodina detorta Walliser

Plate 8, fig. 6

1957 *Lonchodina* n. sp. (a) Walliser: 39, pl. 3, figs 29, 30.
1964 *Lonchodina detorta* Walliser: 43, pl. 9, fig. 20; pl. 30, figs 34–37.
1969 *Ligonodina elegans* Walliser; Jeppsson (*partim*): 21, text-fig. 4D.

Material. 27 specimens: figured (X.686).

Occurrence. Fronian and Telychian.

Description. The straight cusp is laterally compressed and inclined posteriorly. The anterior branch is bowed and bears laterally compressed denticles that may be discrete or partially fused. A little to the posterior of the cusp, the posterior branch is abruptly bent and flexed. The denticles of the posterior branch are discrete. The two branches are of approximately equal length. The shallow basal cavity is flared beneath the cusp and continues as a groove under the anterior branch.

Lonchodina fluegeli Walliser

Plate 8, fig. 7

1964 *Lonchodina fluegeli* Walliser: 44, pl. 6, fig. 4; pl. 32, figs 22–24.
1966 *Lonchodina fluegeli* Walliser; Spasov & Filipović: 42, pl. 2, fig. 10.

Material. 21 specimens: figured (X.687).

Occurrence. Late Fronian and early Telychian.

Description. The cusp is straight, laterally compressed and inclined posteriorly. The anterior branch is straight and bears closely packed, laterally compressed denticles. The posterior branch is slightly bent downwards and inwards and is strongly twisted, so that at the posterior tip the denticles lie in a plane almost at right angles to the plane of the anterior branch. The denticles of the posterior branch are flat and closely packed. A narrow, shallow basal groove that extends beneath both branches is widened only very slightly below the cusp.

REMARKS. All the specimens exhibit strongly twisted posterior branches and the less bent variety noted by Walliser (1964) is not recorded.

Lonchodina greilingi Walliser

Plate 8, fig. 4

1957 *Lonchodina greilingi* Walliser: 38, pl. 3, figs 20–26.
1960 *Lonchodina greilingi* Walliser; Walliser: 31, pl. 8, figs 17, 18.
1960 *Lonchodina greilingi* Walliser; Ziegler: 188, pl. 14, figs 15, 16, 18, 20.
1962 *Lonchodina greilingi* Walliser; Ethington & Furnish: 1274, pl. 173, fig. 10.
1964 *Lonchodina greilingi* Walliser; Walliser: 44, pl. 8, fig. 7; pl. 30, figs 7–9.
1965 *Lonchodina greilingi* Walliser; Philip: 104, pl. 9, fig. 22.
1966 *Lonchodina greilingi* Walliser; Barnett *et al.*: pl. 58, fig. 8.
1969 *Lonchodina greilingi* Walliser; Philip: 292, pl. 17, figs 17, 18, 21; text-fig. 1e.

MATERIAL. 41 specimens: figured (X.688).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is tall, slender, inwardly inclined and circular in transverse section. Each branch bears four to six widely spaced denticles and is slightly twisted near the cusp. Together the branches form an asymmetrical arch. The base of the cusp is moderately deeply excavated and the cavity flares inwardly. The aboral surface of each branch is grooved.

REMARKS. Some specimens are readily identifiable as *L. greilingi*, but several specimens that display transition towards other forms are present and the limits of the species are indistinct. As noted by Walliser (1964 : 44), there are transitional forms towards *Trichonodella inconstans*, *Synprioniodina silurica* and representatives of the genus *Plectospathodus*.

Lonchodina walliseri Ziegler

Plate 8, fig. 5

1957 *Lonchodina* n. sp. (b) Walliser: 40, pl. 3, figs 27, 28.
1960 *Lonchodina walliseri* Ziegler: 188, pl. 14, figs 2, 6, 7.
1964 *Lonchodina walliseri* Ziegler; Walliser: 44, pl. 8, fig. 17; pl. 30, figs 26–33.
1965 *Lonchodina walliseri* Ziegler; Philip: 104, pl. 8, fig. 35.
1967 *Lonchodina walliseri* Ziegler; Rexroad: 37, pl. 3, fig. 6.
1968 *Lonchodina walliseri* Ziegler; Nicoll & Rexroad: 40, pl. 4, figs 8, 9.
1969 *Lonchodina walliseri* Ziegler; Philip: 292, pl. 17, fig. 19.

MATERIAL. 85 specimens: figured (X.689).

OCCURRENCE. Idwian to early Wenlock.

Description. The cusp is stout and subcircular in transverse section. The anterior and posterior branches are of similar length and bear discrete denticles, which are slightly laterally compressed. The aboral surface of the unit is flat, widest beneath the cusp and tapers sharply anteriorly and less sharply posteriorly. The basal cavity is in the form of a shallow pit beneath the cusp.

Remarks. A single aberrant specimen bears an additional branch, closely similar in position and morphology to that of the specimen illustrated by Walliser (1964 : pl. 10, fig. 16). The short branch, which diverges from the anterior branch and is directed anteriorly and inwardly, bears two or three fused denticles. The aboral surface of the branch is narrow and is not excavated.

Lonchodina sp. A

Plate 8, fig. 9

Material. 5 specimens: figured (X.690).

Occurrence. Idwian to Telychian.

Description. This species resembles *Lonchodina walliseri* in general morphology, but lacks a cusp. The denticles are more closely packed than is typical for *L. walliseri*.

Lonchodina sp. B

Plate 8, fig. 8

1967 *Lonchodina*? sp. Rexroad: 38, pl. 3, fig. 5.

Material. 15 specimens: figured (X.691).

Occurrence. Fronian and Telychian.

Description. There is no cusp. The blade is sigmoidal and bears about 10 discrete denticles. The denticles at the anterior end are laterally compressed, those of the posterior are subcircular in section. The aboral surface is widest near the midlength of the unit and tapers more sharply anteriorly than posteriorly. A small pit is excavated in the aboral surface, slightly anterior to the midpoint.

Remarks. This species is similar to *Lonchodina* sp. C, but is less bowed and bears fewer denticles. *Lonchodina* sp. B is from earlier strata than *Lonchodina* sp. C, to which it is probably ancestral.

Lonchodina sp. C

Plate 8, fig. 12

Material. 24 specimens: figured (X.692).

Occurrence. C_{3-4} to early Wenlock.

Description. None of the denticles is so well-developed as to be distinguishable as a cusp. The branches are bowed in opposing directions and the posterior section of the unit is bent downwards. The denticles are closely packed and inclined posteriorly, those of the posterior branch being larger than those of the anterior. The aboral surface is flattened below the posterior branch and slightly grooved below the anterior branch. A small pit is situated anterior to the midpoint of the unit.

REMARKS. In several respects this species resembles the lower Devonian species *Lonchodina cristagalli* Ziegler (1960 : pl. 14, fig. 1). Since there are slight morphological differences and there is a wide separation in known stratigraphic occurrence, the specimens from this study are not placed in *L. cristagalli*.

Genus ***NEOPRIONIODUS*** Rhodes & Müller, 1956

TYPE SPECIES. *Prioniodus conjunctus* Gunnel, 1931.

Neoprioniodus costatus costatus Walliser

Plate 5, fig. 22

1964 *Neoprioniodus costatus costatus* Walliser: 48, pl. 6, fig. 14; pl. 28, figs 36–41; text-fig. 6 l–n.
1966 *Neoprioniodus costatus costatus* Walliser; Spasov: pl. 1, fig. 5.
1966 *Neoprioniodus costatus costatus* Walliser; Spasov & Filipović: 42, pl. 1, figs 10, 11.
1968 *Neoprioniodus costatus* Walliser; Nicoll & Rexroad: 40, pl. 5, figs 15, 16.

MATERIAL. 79 specimens: figured (X.654).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The cusp is inclined posteriorly and has sharp anterior and posterior edges. The outer lateral face of the cusp is flat, the inner lateral face is convex and bears a ridge, which is extended into a distinct rib near the base. The posterior bar is laterally thickened immediately beneath the denticle row, which consists of three to eight laterally compressed denticles, fused nearly to their apices. The anterior margin of the cusp is extended downwards as an anticusp, which commonly bears one to five partially fused denticles. In a few specimens the anticusp is not denticulate. The basal cavity is widest and deepest beneath the cusp and extends as a groove beneath the processes. Basal material is often present.

REMARKS. As noted by Walliser (1964), representatives from lower stratigraphic levels have a strongly denticulate anticusp, while those from higher levels possess a poorly denticulate or non-denticulate anticusp. A few aberrant specimens occur in which the anticusp is split to form two adjacent branches.

Neoprioniodus costatus paucidentatus Walliser

Plate 5, figs 20, 21

1964 *Neoprioniodus costatus paucidentatus* Walliser: 48, pl. 4, fig. 23; pl. 28, figs 31–35; text-fig 6 i–k.

MATERIAL. 27 specimens: figured (X.652), (X.653).

OCCURRENCE. Idwian to Telychian (C_5).

Description. The stout cusp is inclined posteriorly and has sharp anterior and posterior edges. The outer lateral face of the cusp is flat or gently convex, the inner lateral face is convex and bears a low ridge. The anterior margin of the cusp is extended downwards to form an anticusp, which in most specimens is poorly denticulate or non-denticulate. The posterior bar is short and bears three to six fused, laterally compressed denticles. The basal cavity is deepest and widest beneath the cusp and continues as a groove under the processes.

Remarks. As noted by Walliser (1964), there is a reduction in the denticulation of the anticusp and in the elevation of the inner lateral ridge with time. This development is similar to that shown by the younger subspecies, *N. costatus costatus*.

Neoprioniodus excavatus (Branson & Mehl)

Plate 5, fig. 25

1933 *Prioniodus excavatus* Branson & Mehl: 45, pl. 3, figs 7, 8.
1957 *Prioniodina excavata* (Branson & Mehl); Walliser: 46, pl. 2, figs 18, 19.
1958 *Prioniodina excavata* (Branson & Mehl); Bischoff & Sannemann: 103, pl. 15, figs 7, 10, 13.
1962 *Prioniodina bicurvata* (Branson & Mehl); Ethington & Furnish: 1283, pl. 173, fig. 17.
1964 *Neoprioniodus excavatus* (Branson & Mehl); Walliser: 49, pl. 8, fig. 4; pl. 29, fig. 26; text-fig. 5c.
1965 *Neoprioniodus excavatus* (Branson & Mehl); Spasov: 28, pl. 1, fig. 10.
1965 *Neoprioniodus excavatus* (Branson & Mehl); Philip: 105, pl. 9, figs 16, 17.
1969 *Hindeodella excavata* (Branson & Mehl); Jeppsson (*partim*): 18, text-figs 1I, 3C.

Material. 60 specimens: figured (X.655).

Occurrence. Idwian to early Wenlock.

Description. The stout, inwardly inclined cusp is slightly compressed laterally and has rounded anterior and posterior margins. The posterior bar is long and strongly downcurved. The aboral surface of the bar is broad. The rounded denticles of the posterior bar may be closely packed or discrete. The anterior bar is very short and is directed slightly outwards, commonly bearing only a single denticle, although two or three may be present. In inner lateral view, the aboral edge is smoothly curved below the junction between the cusp and anterior bar. The cavity is wide and moderately deep beneath the cusp.

Neoprioniodus latidentatus Walliser

Plate 5, fig. 24

1957 *Prioniodina excavata* (Branson & Mehl) Walliser (*partim*): 46, pl. 2, fig. 17 only.
1964 *Neoprioniodus latidentatus* Walliser: 50, pl. 8, fig. 15; pl. 29, figs 34, 35; text-fig. 5b.

Material. 13 specimens: figured (X.656).

Occurrence. Idwian to early Wenlock.

Description The cusp is erect or inwardly bent and has sharp anterior and posterior edges. The posterior bar is straight and inclined slightly downwards, bearing widely-spaced denticles, which are subcircular in transverse section. The aboral edge rises steeply from the base of the anterior edge of the cusp, producing a sharp, acutely angled outline. The basal cavity is deep beneath the cusp and continues as a wide groove to the tip of the posterior bar.

Neoprioniodus multiformis Walliser

Plate 5, fig. 26

1957 *Prioniodina excavata* (Branson & Mehl) Walliser (*partim*): 46, pl. 2, fig. 16 only.
1964 *Neoprioniodus multiformis* Walliser: 50, pl. 8, fig. 10; pl. 29, figs 14, 16–25; text-fig 5a.

MATERIAL. 74 specimens: figured (X.657).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The stout, erect cusp is commonly slightly twisted and has sharp anterior and posterior edges. The posterior bar is long and slightly curved downwards, bearing discrete, closely spaced denticles. An anterior bar may or may not be developed. When developed, the bar is directed somewhat outwardly and bears one to three closely spaced denticles. The cavity is wide and deep beneath the cusp and continues as a wide groove beneath the posterior bar.

REMARKS. Less variation is shown by these specimens than by those from younger strata described by Walliser (1964).

Neoprioniodus planus Walliser

Plate 5, fig. 23

1964 *Neoprioniodus planus* Walliser: 51, pl. 4, fig. 10; pl. 6, fig. 3; pl. 29, figs 12, 13, 15.
1968 *Neoprioniodus planus* Walliser; Igo & Koike: 12, pl. 1, figs 15, 18; pl. 3, fig. 21.
1968 *Neoprioniodus planus* Walliser; Nicoll & Rexroad: 41, pl. 5, figs 11, 12.
1970 *Neoprioniodus planus* Walliser; Pollock, Rexroad & Nicoll: 756, pl. 114, figs 13, 14.

MATERIAL. 68 specimens: figured (X.658).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is very tall and inclined posteriorly, with a sharp, non-denticulate anterior edge. The unit is considerably laterally compressed. The bent posterior bar bears eight to ten discrete or closely packed denticles, which are inclined posteriorly. The shallow basal cavity is widest below the posterior edge of the cusp and continues along the posterior bar, terminating short of the tip.

Neoprioniodus subcarnus Walliser

Plate 5, fig. 17

1964 *Neoprioniodus subcarnus* Walliser: 51, pl. 5, fig. 7; pl. 28, figs 12–18.
1966 *Neoprioniodus subcarnus* Walliser; Spasov & Filipović: 42, pl. 1, figs 8, 9.
1967 *Neoprioniodus subcarnulus* Walliser; Rexroad: pl. 3, fig. 14.
1968 *Neoprioniodus subcarnus* Walliser; Nicoll & Rexroad: 41, pl. 5, fig. 10.
1969 *Neoprioniodus subcarnus* Walliser; Drygant: 53, pl. 1, figs 12–14.

MATERIAL. 68 specimens: figured (X.659).

Occurrence. Telychian (C_5) to early Wenlock.

Description. The cusp is tall, slender and laterally compressed, the inner side being less strongly convex than the outer. The posterior margin is sharp to rounded, the anterior margin is sharp and is extended strongly downwards to form an anticusp. The outer anterior portion of the cusp bears a small ridge towards the base, often extended aborally to form a small free rib. The posterior bar is inclined downwards and bears 10 to 20 laterally compressed denticles. The denticle adjacent to the cusp is comparatively long and in some specimens a large, well-developed denticle is present at, or slightly posterior to, the midpoint of the bar. A shallow basal cavity, occasionally containing basal material, is excavated beneath the cusp, continuing as a groove under the posterior bar.

Remarks. Walliser (1964 : 51) suggested that the larger denticle developed in the posterior bar of some specimens indicated fusion of a conodont of the species *N. subcarnus* with one of the species *Carniodus carnulus*. A similar development is noted in *Carniodus carnus* and *Exochognathus latialatus*.

Neoprioniodus subcarnus shows morphological similarities to *Carniodus carnus*, which possesses a denticulate anterior process in place of the anticusp. Transitional forms between the two species have not been found.

Genus ***NEOSPATHOGNATHODUS*** Nicoll & Rexroad, 1968

Type species. *Neospathognathodus bullatus* Nicoll & Rexroad, 1968.

Neospathognathodus bullatus Nicoll & Rexroad

Plate 3, fig. 15

1968 *Neospathognathodus bullatus* Nicoll & Rexroad: 44, pl. 1, figs 5–7.

Material. 1 specimen: figured (X.604).

Occurrence. Telychian (C_5).

Description. A free blade, consisting of denticles fused nearly to their apices, comprises half the length of the conodont and continues over the platform as a carina, which bends inwards at the posterior end. On the outer side a single nodose lateral process, directed outwards and anteriorly, forms an angle of about 40° with the carina, from which it is separated by a trough. On the inner side a similar nodose process forms an angle of about 20° with the carina and is directed anteriorly. An irregularly nodose, posterior outer lateral process projects from the posterior tip of the carina. Aborally, the lateral processes and the area beneath the carina at their junction are excavated, but basal material masks the depth of the cavity. A groove is excavated beneath the free blade, but the aboral surface of the posterior process shows only a small, shallow excavation.

Neospathognathodus celloni (Walliser)

Plate 3, figs 9–12

1964 *Spathognathodus celloni* Walliser: 73, pl. 4, fig. 13; pl. 14, figs 3–16; text-fig. 1b; text-fig. 7 b–f.
1968 *Spathognathodus celloni* Walliser; Igo & Koike: 18, pl. 2, figs 1–4.
1968 *Neospathognathodus celloni* (Walliser) Nicoll & Rexroad: 45, pl. 2, figs 1–4.

MATERIAL. 176 specimens: figured (X.597), (X.598), (X.599), (X.600).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The straight blade bears erect or slightly posteriorly inclined denticles, commonly fused nearly to their apices. Two offset lateral processes are situated at, or slightly posterior to, midlength. The processes are poorly developed and usually unornamented. The lateral process nearer the posterior tip is often the more extensively flared. The processes are excavated aborally and the cavity extends as a shallow groove to the tips of the blade.

REMARKS. A few specimens, with rudimentary nodes on one lateral process, are transitional to *N. pennatus*.

Neospathognathodus pennatus (Walliser)

Plate 3, figs 13, 16

1964 *Spathognathodus* sp., ex aff. *Sp. celloni* Walliser: 74, pl. 14, figs 17, 18; text-fig. 7a.
1964 *Spathognathodus pennatus angulatus* Walliser (*partim*): 79, pl. 14, fig. 19 only; text-fig. 1c.
1964 *Spathognathodus pennatus pennatus* Walliser: 79, pl. 14, figs 23–26; pl. 15, fig. 1; text-fig. 1d.
1964 *Spathognathodus pennatus procerus* Walliser: 80, pl. 15, figs 2–8; text-fig. 1c.
1966 *Spathognathodus pennatus procerus* Walliser; Spasov & Filipović: 50, pl. 1, fig. 6.
1968 *Spathognathodus pennatus procerus* Walliser; Igo & Koike: 18, pl. 2, figs 8–11.
1968 *Neospathognathodus pennatus* (Walliser) Nicoll & Rexroad: 47, pl. 2, fig. 5.
1969 *Spathognathodus pennatus procerus* Walliser; Schönlaub: pl. 1, fig. 13.
1969 *Spathognathodus pennatus procerus* Walliser; Drygant: 50, pl. 1, figs 2, 3.

MATERIAL. 53 specimens: figured (X.601), (X.602).

OCCURRENCE. Telychian (C_5) to early Wenlock.

DESCRIPTION. The blade is straight or somewhat sigmoidal in oral view and bears erect denticles, fused nearly to their apices. In some specimens the blade is expanded and the denticles nodose. Two offset lateral processes are situated at, or posterior to, midlength of the unit. The process nearer the anterior of the unit is usually unornamented, the other bears a row of denticles that is directed outwardly and anteriorly, making an angle of 45°–70° with the blade. The aboral surface of the blade and processes is deeply excavated.

REMARKS. The close relationship to *Pterospathodus amorphognathoides*, pointed out by Walliser (1964 : 80), is evident. Nicoll & Rexroad (1968 : 48) considered *N. pennatus* to be intermediate between *N. celloni* and *N. bullatus*.

Neospathognathodus? sp.

Plate 3, fig. 14

MATERIAL. 1 specimen: figured (X.603).

OCCURRENCE. Idwian.

DESCRIPTION. The specimen is slightly broken, but consists of a straight blade supporting two lateral processes, situated almost opposite each other. The broken blade bears eight denticles, one of which is noticeably, though not greatly, larger than the others. The lateral processes arise below the main denticle and are directed almost perpendicularly away from the blade. One process is unornamented, the other bears three discrete, sharp denticles that are strongly inclined parallel to the blade. The entire aboral surface is excavated, the cavity being deepest under the main denticle.

REMARKS. The morphology of this specimen is consistent with an assignment to *Neospathognathodus*, but the anomalous stratigraphic occurrence renders such an assignment questionable. This specimen is from strata of high Idwian age, whereas *Neospathognathodus* otherwise makes its first appearance in the Welsh Borderland in strata of Telychian (C_5) age. Of the younger species of *Neospathognathodus* the specimen most resembles *N. pennatus*.

Genus *OZARKODINA* Branson & Mehl, 1933

TYPE SPECIES. *Ozarkodina typica* Branson & Mehl, 1933.

Ozarkodina adiutricis Walliser

Plate 5, figs 2, 3

1964 *Ozarkodina adiutricis* Walliser: 54, pl. 4, fig. 14; pl. 27, figs 1–10; text-fig. 1a; text-fig. 7h, i, k–m.
1968 *Ozarkodina adiutricis* Walliser; Nicoll & Rexroad: 48, pl. 2, figs 6–8.
1969 *Ozarkodina adiutricis* Walliser; Schönlaub: pl. 1, fig. 18.

MATERIAL. 9 specimens: figured, S.3.12, (X.631).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. The tall cusp is inclined posteriorly and is situated somewhat posterior of midlength. The anterior part of the blade is much higher than the posterior and bears four to six denticles, which are fused nearly to their apices. The posterior part of the blade bears two to four low denticles. The entire aboral surface is excavated, the cavity being deepest beneath the cusp. The cavity is commonly extended laterally beneath the cusp on one side and is enclosed by a flaring lip.

Ozarkodina alisonae sp. nov.

Plate 5, figs 4, 6

DERIVATION OF NAME. After my wife, Alison.

Diagnosis. *Ozarkodina* Branson and Mehl with a cusp that is much taller and broader than the other denticles of the blade. The blade is arched and bowed, and possesses anterior and posterior portions of approximately equal length and height. The denticles are of uniform size and fused nearly to their apices. The basal cavity is situated beneath the cusp and is flanked by lips that flare laterally and aborally.

Holotype. Specimen (X.581).

Material. 34 specimens: figured (X.581), (X.582).

Type locality and horizon. The Wych Formation of Gullet Quarry, sample Gullet 2.

Occurrence. Telychian (C_5).

Description. The unit is strongly bowed and arched. In lateral view, the anterior and posterior parts of the blade form an angle of 100°–160°. The cusp is situated at midlength of the unit and is tall, sharply pointed and slightly inclined posteriorly. The anterior and posterior edges of the cusp are sharp and the lateral faces flat or gently convex. The anterior part of the blade bears four to nine laterally compressed denticles, which are fused nearly to their apices and decrease only a little in height anteriorly. The denticles nearest the cusp are more or less erect, those at the anterior end are directed a little anteriorly. The posterior part of the blade bears five to nine laterally compressed and almost completely fused denticles, which are more slender than those of the anterior. The denticles are inclined posteriorly and are of subequal height. A rounded basal cavity is situated beneath the cusp and is flanked by lips that flare laterally and aborally. The cavity is extended as a groove beneath the blade.

Remarks. This species is easily distinguished from other Llandovery species of *Ozarkodina* by the strong arching and bowing of the unit and by the prominently flared lips of the basal cavity. There is a fairly close similarity to younger specimens of *O. typica*, which possess a larger number of more slender denticles and do not display flared lips to the basal cavity. There is also a morphological resemblance to *O. jaegeri* Walliser (1964 : 57, pl. 25, figs 11–18), but there is no evidence of a phylogenetic link.

It is possible that the specimens referred by Igo & Koike (1968 : 8, pl. 2, fig. 7) to *Bryantodus* sp. belong here.

***Ozarkodina* cf. *O. edithae* Walliser**

Plate 4, fig. 17

cf. 1964 *Ozarkodina edithae* Walliser: 55, pl. 26, figs 12–18.
1970 *Ozarkodina* cf. *O. edithae* Walliser; Pollock, Rexroad & Nicoll: 756, pl. 113, figs 1–4.

Material. 37 specimens: figured (X.632).

Occurrence. Idwian to Telychian (C_5).

Description. The blade is flat with an aboral margin that is straight or very feebly arched. The anterior part of the blade bears fused denticles, increasing in height regularly towards the cusp. The tips of the denticles and of the cusp form a straight line. The posterior part of the blade is lower and the denticles are partially or almost completely fused. The denticles decrease in height posteriorly. The basal cavity is small and only slightly flared beneath the cusp.

Remarks. Pollock, Rexroad & Nicoll (1970 : 756) noted that their specimens had a less angular oral outline than those illustrated by Walliser (1964). This is also true of the specimens from this study. As there are slight morphological differences, and because the stratigraphic ranges have not been shown to be continuous, the Llandovery specimens are not, at present, placed with certainty in *O. edithae*.

Ozarkodina gaertneri Walliser

Plate 5, figs 5, 7

1964 *Ozarkodina gaertneri* Walliser: 57, pl. 6, fig. 6; pl. 27, figs 12–19; text-fig. 1g.
1966 *Ozarkodina gaertneri* Walliser; Spasov & Filipović: 44, pl. 1, figs 1, 2.
1968 *Ozarkodina gaertneri* Walliser; Igo & Koike: 14, pl. 1, figs 5–9.
1968 *Ozarkodina gaertneri* Walliser; Nicoll & Rexroad: 49, pl. 2, figs 12–14.
1969 *Ozarkodina gaertneri* Walliser; Schönlaub: pl. 1, fig. 15.

Material. 220 specimens: figured (X.633), (X.634).

Occurrence. Telychian (C_5) to early Wenlock.

Description. The unit is arched and slightly bowed. The strong cusp is situated near midlength and is inclined posteriorly. The transverse section of the cusp is lenticular. The denticles of the blade are laterally compressed and partially fused. Those to the posterior of the cusp are lower than those to the anterior. The blade is laterally thickened below the denticle row to form a narrow platform. On one side the aboral edge of the blade is projected downwards beneath the cusp to form a prominent lip. The aboral surface of the blade is grooved and the cavity is enlarged beneath the cusp.

Remarks. Transition from *O. adiutricis* is shown by specimens from strata of C_5 age, which display less thickening and possess a less well-developed aboral lip than those from younger levels.

Ozarkodina hanoverensis Nicoll & Rexroad

Plate 5, fig. 1

1968 *Ozarkodina hanoverensis* Nicoll & Rexroad: 50, pl. 2, fig. 9

Material. 2 specimens: figured (X.635).

Occurrence. Telychian (C_5).

Description. The unit is slightly arched and bowed. The cusp is broad, slightly posteriorly inclined and situated near midlength. The anterior part of the blade bears five denticles that are closely packed, but not fused. The posterior part bears seven closely packed denticles. The cavity is small beneath the cusp and is slightly flared on the inner side. Grooves extend a short distance anteriorly and posteriorly from the cavity.

Ozakodina media Walliser

Plate 4, fig. 21

1953 *Ozarkodina* sp. Rhodes: pl. 23, fig. 244.
1957 *Ozarkodina media* Walliser: 40, pl. 1, figs 21–25.
1958 *Ozarkodina media* Walliser; Bischoff & Sannemann: 99, pl. 14, figs 15, 16, 18, 19, 21.
1962 *Ozarkodina media* Walliser; Ethington & Furnish: 1278, pl. 173, fig. 9.
1962 *Ozarkodina media* Walliser; Spasov & Veselinović: 240, pl. 1, figs 6, 8, 14.
1964 *Ozarkodina media* Walliser; Walliser: 58, pl. 8, fig. 5; pl. 26, figs 19–34.
1965 *Ozarkodina media* Walliser; Philip: 106, pl. 9, figs 1, 3.
1966 *Ozarkodina media* Walliser; Barnett *et al.*: pl. 58, fig. 21.
1966 *Ozarkodina media* Walliser: Spasov & Filipović: 44, pl. 2, fig. 7.
1966 *Ozarkodina media* Walliser; Spasov: pl. 1, fig. 2.
1966 *Ozarkodina media* Walliser; Philip: 447, pl. 1, figs 29, 32, 33.
1968 *Ozarkodina media* Walliser; Igo & Koike: 15, pl. 3, fig. 5.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppsson (*partim*): 18, text-figs 1H, 3B.

MATERIAL. 112 specimens: figured (X.636).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is tall, laterally compressed and curved posteriorly. The anterior and posterior parts of the blade are of approximately equal length, but the anterior is deeper. The denticles are laterally compressed and closely packed, those of the anterior being a little larger than those of the posterior. The arch of the blade, in lateral view, is between 120° and 180°. The basal cavity is wide and flared beneath the cusp and extends as a groove to the tips of the blade.

REMARKS. The recognition of *O. media* in this study extends the known stratigraphic range of the species downwards to the upper part of the Idwian. Walliser (1964) described and illustrated the wide variation shown by specimens from the *patula*-Zone (Wenlock) to the lower Devonian. Much less variation is apparent in the older specimens from the present study.

Ozarkodina typica Branson & Mehl

Plate 4, figs 18–20

1933 *Ozarkodina typica* Branson & Mehl: 51, pl. 3, figs 43–45.
1953 *Ozarkodina typica* Branson & Mehl; Rhodes: 320, pl. 23, figs 251, 261, 262.
1964 *Ozarkodina typica typica* Branson & Mehl; Walliser: 61, pl. 9, fig. 21; pl. 25, figs 20, 21; pl. 26, figs 1, 2.
1967 *Ozarkodina typica* Branson & Mehl; Rexroad: 39, pl. 2, figs 7, 8.
1970 *Ozarkodina typica* Branson & Mehl; Pollock, Rexroad & Nicoll: 757, pl. 113, figs 16–18.

MATERIAL. 22 specimens: figured (X.637), (X.638), (X.639).

OCCURRENCE. Idwian to early Wenlock.

Description. The unit is arched and slightly bowed. The cusp is tall and posteriorly inclined, with sharp anterior and posterior edges. The anterior part of the blade bears eight to eleven slender, laterally compressed, posteriorly inclined denticles, fused nearly to their apices. The posterior part is commonly shorter and bears six to ten partially fused denticles, which may be lower than those of the anterior. The aboral surface is grooved from tip to tip, the cavity deepening and widening beneath the cusp, where it is flanked by slightly laterally flared lips.

Remarks. As noted by Pollock *et al.* (1970 : 757), lower Silurian representatives of this species are shorter than those from younger strata. In other respects, however, these specimens are comparable with those illustrated by Branson and Mehl (1933), although the possibility of homeomorphy cannot be disregarded.

Genus ***PALTODUS*** Pander, 1856

Type species. *Paltodus subaequalis* Pander, 1856.

Paltodus costulatus Rexroad

Plate 9, fig. 21

1967 *Paltodus costulatus* Rexroad: 40, pl. 4, figs 26–29.
1968 *Paltodus costulatus* Rexroad; Nicoll & Rexroad: 51, pl. 7, figs 16–18.
1970 *Paltodus costulatus* Rexroad; Pollock, Rexroad & Nicoll: 757, pl. 114, figs 29, 30.

Material. 68 specimens: figured (X.728).

Occurrence. Fronian to early Wenlock.

Description. The small cone is slightly curved and bowed. The anterior and posterior edges are sharp. The posterior portion of each lateral face bears a poorly developed costa. The base is entirely excavated and the cavity terminates at a point at about one-third of the length of the cone.

Paltodus debolti Rexroad

Plate 9, fig. 18

1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 20–22 only.
1967 *Paltodus debolti* Rexroad: 41, pl. 4, figs 22–25.
1968 *Paltodus debolti* Rexroad; Nicoll & Rexroad: 52, pl. 7, fig. 26.
1970 *Paltodus debolti* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, figs 32, 33.

Material. 63 specimens: figured (X.725).

Occurrence. C_{3-4} to early Wenlock.

Description. The cone is curved and asymmetrical. The convex antero-lateral face is bounded by prominent costae at its anterior and posterior margins. A less well-developed costa is situated in the centre of the face. On the inner side a flat lateral face is bordered by the anterior costa and a second posterior costa. The base is entirely excavated, the cavity extending for about half the length of the cone.

Paltodus dyscritus Rexroad

Plate 9, fig. 19

1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 6?, 17–19 only.
1967 *Paltodus dyscritus* Rexroad: 42, pl. 4, figs 30–34.
1968 *Paltodus dyscritus* Rexroad; Nicoll & Rexroad: 52, pl. 7, figs 31–33.
1970 *Paltodus dyscritus* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, fig. 31.

MATERIAL. 102 specimens: figured (X.726).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The curved cone is nearly symmetrical. The anterior face is gently convex, almost flat, and is flanked on each side by a prominent antero-lateral costa. The lateral faces are flat to gently concave, and become broad towards the base. The posterior margin bears two or three costae. The base is entirely excavated, the cavity extending for half the length of the cone.

Paltodus migratus Rexroad

Plate 9, fig. 20

1967 *Paltodus migratus* Rexroad: 44, pl. 4, figs 17–21.
1968 *Paltodus migratus* Rexroad; Nicoll & Rexroad: 52, pl. 7, fig. 27.
1970 *Paltodus migratus* Rexroad; Pollock, Rexroad & Nicoll: 758, pl. 114, fig. 34.

MATERIAL. 53 specimens: figured (X.727).

OCCURRENCE. Idwian to Telychian (C_5).

DESCRIPTION. The cone is curved, laterally compressed and only slightly asymmetrical. The anterior and posterior edges are costate. Each lateral face bears two prominent costae, one central and one posterior of centre. These costae may bifurcate and there may be additional poorly-developed costae. The entire base is excavated and the cavity extends for about half the length of the cone.

Genus ***PANDERODUS*** Ethington, 1959

TYPE SPECIES. *Paltodus unicostatus* Branson & Mehl, 1933.

Panderodus cf. ***P. gracilis*** (Branson & Mehl)

Plate 9, figs 12, 13

cf. 1933 *Paltodus gracilis* Branson & Mehl: 108, pl. 8, figs 20, 21.

MATERIAL. 187 specimens: figured (X.722), (X.723).

OCCURRENCE. Idwian to Telychian (C_5).

DESCRIPTION. The cone is curved posteriorly and has a broadly rounded anterior margin and a sharp posterior edge. The posterior portion of the cone is laterally compressed and is separated from the anterior portion by a sharp offset on each lateral face, originating at, or near, the base. The basal cavity is conical and extends for half the length of the cone.

REMARKS. Most of the specimens from this study show less antero-posterior extension near the base than displayed by the specimens of *P. gracilis* illustrated by Branson & Mehl (1933). There is a closer resemblance to those illustrated by Glenister (1957 : pl. 85, figs 2–5).

Panderodus gracilis has not previously been recorded from strata of younger than upper Ordovician age. The oldest specimens from this study are of Idwian age and there is, at present, no evidence of continuity of stratigraphic range. As it is possible that the Llandovery specimens are homeomorphic with those from the Ordovician, they are not positively included in *P. gracilis*.

Panderodus serratus Rexroad

Plate 9, fig. 7

1967 *Panderodus unicostatus serratus* Rexroad: 47, pl. 4, figs 3, 4.

MATERIAL. 240 specimens: figured specimen (X.718).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The cone is curved and asymmetrical. The anterior margin is rounded, the posterior edge is sharp and ornamented by a row of germ denticles for about two-thirds of its length. The lateral costa on one face is more strongly developed than on the other. In lateral view, the unit is broad and flat near the base, becoming more slender towards the apex. The basal cavity is deep and conical.

REMARKS. Rexroad (1967) remarked that this form differed only in the possession of a denticulate posterior margin from *P. unicostatus* (Branson & Mehl) and consequently named it as a subspecies of that species. The specimens recovered in the present study are similar to those illustrated by Rexroad and resemble only the broader, flatter specimens of *P. unicostatus*, which represent one extreme of the variation range of that species. Rexroad recorded only a few specimens from a very limited stratigraphic horizon, but in Britain the species is common throughout the Idwian to Telychian, where it occurs in association with *P. unicostatus*.

It is probable that *P. denticulatus* Schwab from the upper Silurian Aymestry Limestone (Schwab 1969 : 521–525, text-figs 1, 2) belongs here, but in view of the gap in stratigraphic ranges it is not at present included in synonymy.

Panderodus simplex (Branson & Mehl)

Plate 9, figs 8, 9

1933 *Paltodus simplex* Branson & Mehl: 42, pl. 3, fig. 4.
1947 *Paltodus acostatus* Branson & Branson (*partim*): 554, pl. 82, figs 1–5 only.

1953 *Paltodus acostatus* Branson & Branson; Rhodes: 296, pl. 21, figs 111, 112; pl. 22, figs 163, 164; pl. 23, figs 212, 213.
1957 *Paltodus*? *acostatus* Branson & Branson; Glenister: 727, pl. 85, fig. 7.
1960 *Paltodus* cf. *P. acostatus* Branson & Branson; Walliser: 31, pl. 7, fig. 10.
1961 *Paltodus acostatus* Branson & Branson: Bergström: 48, pl. 1, figs 13, 14.
1964 *Panderodus acostatus* (Branson & Branson); Serpagli & Greco: 204, pl. 36, figs 4a, 4b.
1966 *Panderodus simplex* (Branson & Mehl); Clark & Ethington: 682, pl. 82, figs 10, 14.
1967 *Panderodus simplex* (Branson & Mehl); Rexroad: 45, pl. 4, figs 7, 8.
1968 *Panderodus simplex* (Branson & Mehl); Nicoll & Rexroad: 54, pl. 7, fig. 28.
1969 *Panderodus simplex* (Branson & Mehl); Philip: 294, pl. 17, figs. 2, 3, 5, 12, text-fig. 1c.
1970 *Panderodus simplex* (Branson & Mehl); Pollock, Rexroad & Nicoll: 758, pl. 114, figs 23–25.

MATERIAL. 1,465 specimens: figured (X.719), (X.720).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is moderately curved and strongly laterally compressed. The anterior and posterior edges are sharp and the transverse section of the cone is lenticular. The basal cavity extends for about two-thirds of the length of the cone, terminating at a point close to the anterior margin.

***Panderodus* cf. *P. staufferi* (Branson, Mehl & Branson)**

Plate 9, fig. 10

cf. 1951 *Paltodus staufferi* Branson, Mehl & Branson: 7, pl. 1, figs 23–27

MATERIAL. 332 specimens: figured (X.721).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cone is curved posteriorly and has sharp anterior and posterior edges. The anterior edge is commonly keeled from a point just above the base to the point of maximum recurvature, at about midlength of the cone. Each lateral face bears a costa, which is variable in position and development, but in no case extends to the base. The basal cavity is deep and conical, extending for about half the length of the cone.

REMARKS. These specimens are less antero-posteriorly extended at the base than those illustrated by Branson, Mehl & Branson (1951). *P. staufferi* has previously been recorded only from the upper Ordovician and it is possible that the Llandovery specimens represent homeomorphs of the Ordovician forms.

***Panderodus unicostatus* (Branson & Mehl)**

Plate 9, figs 5, 6

1933 *Paltodus unicostatus* Branson & Mehl: 42, pl. 3, fig. 3.
1947 *Paltodus unicostatus* Branson & Mehl; Branson & Branson (*partim*): 554, pl. 82, figs 11–16 only.
1953 *Paltodus unicostatus* Branson & Mehl; Rhodes: 298, pl. 21, figs 84–88; pl. 22 figs 155, 156; pl. 23 figs 214–216.
1955 *Paltodus* cf. *P. unicostatus* Branson & Mehl; Rhodes: 127 pl. 10 figs 1, 3.

1957 *Paltodus? unicostatus* Branson & Mehl; Glenister: 729 pl. 85, fig. 1.
1957 *Paltodus unicostatus* Branson & Mehl; Walliser: 43, pl. 2, fig. 1.
1959 *Panderodus unicostatus* (Branson & Mehl); Sweet *et al.*: 1057, pl. 131, fig. 3.
1961 *Panderodus unicostatus* (Branson & Mehl); Wolska: 353, pl. 4, figs 3a, b.
1962 *Panderodus unicostatus* (Branson & Mehl); Kockel & Stoppel: 161, pl. 1, fig. 2.
1962 *Panderodus unicostatus* (Branson & Mehl); Sweet & Bergström: 1234, text-fig. 1d.
1964 *Panderodus unicostatus* (Branson & Mehl); Serpagli & Greco: 206, pl. 36, fig. 7; pl. 37, figs 1a, b.
1964 *Panderodus* cf. *unicostatus* (Branson & Mehl); Hamar: 272, pl. 1, figs 28, 29.
1965 *Panderodus unicostatus* (Branson & Mehl); Merrill: 390, pl. 2, fig. 8.
1965 *Panderodus unicostatus* (Branson & Mehl); Brooks & Druce: 376, pl. 12, fig. 8.
1966 *Panderodus unicostatus* (Branson & Mehl); Hamar: 67, pl. 1, fig. 6.
1966 *Panderodus unicostatus* (Branson & Mehl); Winder: pl. 9, fig. 7.
1966 *Panderodus unicostatus* (Branson & Mehl); Clark & Ethington: 683, pl. 82, figs 17, 19.
1966 *Panderodus unicostatus* (Branson & Mehl); Philip: 447, pl. 1, figs 10–12, 19.
1967 *Panderodus unicostatus unicostatus* (Branson & Mehl); Rexroad: 46, pl. 4, figs 1, 2.
1968 *Panderodus unicostatus unicostatus* (Branson & Mehl); Nicoll & Rexroad: 54, pl. 7, figs 29, 30.
1969 *Panderodus unicostatus* (Branson & Mehl); Philip: 295, pl. 17, figs 1, 4, 13, 14, text-fig. 1d.
1970 *Panderodus unicostatus unicostatus* (Branson & Mehl); Pollock, Rexroad & Nicoll: 758, pl. 114, figs 26–28.

MATERIAL. 3,750 specimens: figured (X.716), (X.717).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The asymmetric cone is curved, with a rounded anterior margin and a sharp posterior edge. The lateral costa on one face is more strongly developed than on the other. There is a variation from slender to robust forms. The basal cavity extends for about two-thirds of the length of the cone.

Panderodus sp. A

Plate 9, fig. 11

MATERIAL. 117 specimens: figured (X.724).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The stout cone is strongly recurved posteriorly at about half its length. The anterior margin is broadly rounded, the posterior margin sharply rounded. The base is only a little extended antero-posteriorly. The posterior portion is laterally compressed and is separated from the anterior portion by a sharp offset on each lateral face. The deep basal cavity terminates at the point of maximum recurvature.

REMARKS. The relationships of these specimens are difficult to determine. Rexroad (1967 : pl. 4, figs 5, 6) illustrated two specimens similar to those described above and assigned them to *Panderodus* cf. *P. unicostatus*. It is possible that these do represent an extreme variant of *P. unicostatus*, but there do not appear to be any intermediate forms in the Welsh Borderland material. Morphologically similar conodonts from the upper Ordovician were referred to *P. robustus* by Branson, Mehl & Branson (1951 : 8, pl. 1, figs 28–33).

Genus *PLECTOSPATHODUS* Branson & Mehl, 1933

TYPE SPECIES. *Plectospathodus flexuosus* Branson & Mehl, 1933.

REMARKS. The orientation of the genus *Plectospathodus* has been the subject of some discussion by previous authors. Branson & Mehl (1933) did not define the orientation of their specimens, but compared the genus to *Ozarkodina*, in which the limbs are anterior and posterior. Rhodes (1953) considered that the processes were lateral, a view endorsed in 1957 by Walliser, who pointed out that with this orientation the cusp is recurved posteriorly. In 1964, however, Walliser described several species of *Plectospathodus* orientated such that the limbs were anterior and posterior. Rexroad (1967) pointed out the close relationship between *Plectospathodus* and *Trichonodella* and applied the same orientation, with the processes lateral, to each genus. Transitions between species of *Plectospathodus* and *Trichonodella* are apparent and the orientation applied by Rexroad is followed here.

Plectospathodus extensus Rhodes

Plate 7, figs 21, 22

1953 *Plectospathodus extensus* Rhodes: 323, pl. 23, figs 236–240
1957 *Plectospathodus extensus* Rhodes; Walliser: 43, pl. 3, figs 1, 2.
1958 *Plectospathodus extensus* Rhodes; Bischoff & Sannemann: 101, pl. 15, figs 11, 14, 15.
1960 *Plectospathodus extensus* Rhodes; Walliser: 32, pl. 8, fig. 20.
1962 *Plectospathodus extensus* Rhodes; Ethington & Furnish: 1281, pl. 173, fig. 6.
1962 *Plectospathodus extensus* Rhodes; Spasov & Veselinović: 241, pl. 2, fig. 4.
1964 *Plectospathodus extensus* Rhodes; Walliser: 64, pl. 8, fig. 1; pl. 30, figs 13, 14.
1965 *Plectospathodus extensus* Rhodes; Philip: 110, pl. 9, figs 9, 10.
1966 *Plectospathodus extensus* Rhodes; Barnett *et al.*: pl. 58, fig. 13.
1966 *Plectospathodus extensus* Rhodes; Spasov & Filipović: 47, pl. 2, figs 13, 17.
1968 *Plectospathodus extensus* Rhodes; Igo & Koike: 15, pl. 3, fig. 12.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppsson (*partim*): 18, text-figs 1K, 3E.

MATERIAL. 41 specimens: figured (X.675), (X.676).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is slender, sharp, posteriorly curved and circular in transverse section. The lateral processes may be straight or curved and are bowed posteriorly. One lateral process bears discrete denticles of subequal size, the other discrete denticles of unequal size, the largest being developed at the tip. The aboral margin of the cusp is extended posteriorly to form a prominent lip. The cavity is broadest and deepest beneath the cusp and extends as a shallow groove on the aboral surfaces of the lateral processes.

REMARKS. The recovery of *P. extensus* from the Llandovery of the Welsh Borderland extends the known stratigraphic range of the species down to the Fronian.

Plectospathodus flexuosus Branson & Mehl

Plate 7, fig. 24

1933 *Plectospathodus flexuosus* Branson & Mehl: 47, pl. 3, figs 31, 32.
1953 *Plectospathodus elegans* Rhodes: 323, pl. 23, figs 255, 263, 264.
1964 *Plectospathodus flexuosus* Branson & Mehl; Walliser: 65, pl. 9, fig. 10; pl. 30, figs 15, 16.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1E, 2E, $2E_2$.
1970 *Plectospathodus flexuosus* Branson & Mehl; Pollock, Rexroad & Nicoll: 758, pl. 113, figs 19, 20.

MATERIAL. 9 specimens: figured (X.677).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The erect cusp is elliptical in transverse section, with the lateral diameter greatest. The lateral processes are thin, deep and of unequal length. The shorter process bears flat denticles, fused nearly to their apices and of unequal size, the largest being situated near midlength. The longer process is flexed posteriorly and bears short, flat denticles, fused nearly to their apices. The aboral surface is excavated only beneath the cusp, where a shallow, scarcely flared pit is present.

Plectospathodus irregularis (Branson & Branson)

Plate 7, fig. 23

1947 *Prioniodina irregularis* Branson & Branson: 555, pl. 82, figs 30, 31.
1967 *Plectospathodus irregularis* (Branson & Branson); Rexroad: 48, pl. 3, fig. 15.

MATERIAL. 5 specimens: figured (X.678).

OCCURRENCE. Fronian.

DESCRIPTION. The cusp is tall, posteriorly curved and subcircular in transverse section. The lateral processes are of unequal length, the shorter bearing two or three denticles of subequal size. The longer process is flexed a little posteriorly and bears five shorter, discrete denticles. The aboral surface of each process is grooved and the cavity widens and deepens beneath the cusp.

REMARKS. These specimens differ from those described by Branson & Branson (1947) in possessing a greater number of denticles on the longer lateral process and, in one example, an additional denticle on the shorter process. In all other features the specimens are comparable.

Genus ***PTEROSPATHODUS*** Walliser, 1964

TYPE SPECIES. *Pterospathodus amorphognathoides* Walliser, 1964.

Pterospathodus amorphognathoides Walliser

Plate 3, figs 17–19

1964 *Pterospathodus amorphognathoides* Walliser: 67, pl. 6, fig. 7; pl. 15, figs 9–15; text-fig. 1f.

1964 *Spathognathodus pennatus angulatus* Walliser (*partim*): 79, pl. 14, figs 21, 22 only.
1966 *Pterospathodus amorphognathoides* Walliser; Spasov & Filipović: 48, pl. 1, figs 4, 5.
1966 *Pterospathodus amorphognathoides* Walliser; Spasov: pl. 1, fig. 1.
1968 *Pterospathodus amorphognathoides* Walliser; Igo & Koike: 16, pl. 2, figs 12, 13.
1968 *Pterospathodus amorphognathoides* Walliser; Nicoll & Rexroad: 56, pl. 3, figs 1–7.
1969 *Pterospathodus amorphognathoides* Walliser; Schönlaub: pl. 1, fig. 8.
1969 *Pterospathodus amorphognathoides* Walliser; Drygant: 49, pl. 1, fig. 6.

MATERIAL. 174 specimens: figured (X.605), (X.606), (X.607).

OCCURRENCE. Telychian (C_6) and early Wenlock.

DESCRIPTION. The unit consists of a nearly straight blade with a bifurcating inner lateral process situated at, or slightly anterior to, midlength. A small outer lateral process may be situated directly opposite, or somewhat anterior to, the inner lateral process. The blade is commonly laterally thickened in mature specimens to form a narrow platform, bearing up to 40 closely packed, rounded denticles, which are often higher and sharper at the anterior end. The denticles are rounded in cross-section, but in large specimens become compressed and are extended laterally, particularly near the junction of the blade with the inner lateral process. In specimens showing marked platform development the denticle row may be bordered by a narrow trough on each side. The blade may be bent outwards at the posterior end. The inner lateral process consists of two branches, the longer of which is directed inwards and anteriorly and bears up to 10 low denticles. The shorter, posteriorly directed branch bears one to five low denticles. The branches diverge from the blade at angles that vary from 25° to 70°, but may be separated from it by a low ridge, which is itself perpendicular to the blade. In specimens where the blade is thickened to form a platform, the branches of the inner lateral process are similarly thickened. The small outer lateral process may be in the form of a trough-like lateral extension of the thickened blade. In other specimens it is low and unornamented, but in large examples it may support a small number of denticles. A wide, deep basal groove, commonly containing basal material, underlies the blade and the lateral processes.

REMARKS. Mature specimens show a large range of variation and marked differences are apparent between forms from the late Llandovery and those from the early Wenlock. In the Telychian (C_6), all but the smallest specimens display thickening of the blade into a platform and mature specimens possess a large number of denticles (Pl. 3, figs 18, 20). In the material from the Wenlock Shale the adults are morphologically closer to the juveniles and develop a smaller number of denticles. There is no thickening of the blade, which is usually separated from the inner lateral process by a low ridge (Pl. 3, fig. 19). If this sequence is observed elsewhere, it may be possible to define two chronological subspecies of *P. amorphognathoides*.

Genus ***PYGODUS*** Lamont & Lindström, 1957

TYPE SPECIES. *Pygodus anserinus* Lamont & Lindström, 1957.

REMARKS. There has been some controversy about the identification of the specimens described by Lamont & Lindström (1957) as conodonts. The genus

Pygodus was rejected from the Conodontophorida in the *Treatise on Invertebrate Paleontology* (Hass 1962 : W65) and included in the Paraconodontida (1962 : W248). Sweet & Bergström (1962 : 1250), however, stated that representatives of *Pygodus* grew similarly to all other conodonts and Lindström (1964 : 20, fig. 5C : 26, fig. 7E) showed that *Pygodus* had the structure of a true conodont. Rhodes & Müller (1966 : 4) still voiced doubts about the genus and suggested that further histological investigation was necessary before it could be assigned with certainty to the Conodontophorida.

Pygodus*? *lyra Walliser

Plate 3, fig. 2

1964 *Pygodus lyra* Walliser: 68, pl. 5, fig. 5; pl. 12, figs 8–14.

MATERIAL. 19 specimens: figured (X.609).

OCCURRENCE. Telychian (C_5).

DESCRIPTION. Two corrugated ridges diverge from the short free blade to form a lyre shape. In some specimens the blade bisects the angle between the two ridges and bilateral symmetry is approached, but in others the blade is not central and is continuous with one of the ridges. A low, but prominent carina, dipping posteriorly, is present between the two ridges, from which it is separated by an unornamented trough on each side. This carina continues beyond the posterior limit of the rest of the unit forming a sharp posterior tip. The entire aboral surface is deeply excavated.

REMARKS. These specimens differ in several respects from those described by Walliser (1964), which do not possess a marked central carina and display an indented posterior termination. Walliser mentioned that some of his larger specimens possessed a central ridge, but in the present material specimens of all sizes display this feature. The side ridges exhibited by some of Walliser's specimens (e.g. Walliser 1964 : pl. 12, fig. 12) are absent. Despite these differences, these specimens appear to be conspecific with Walliser's, and may represent geographical or successional variants.

No phylogenetic link has been demonstrated between Ordovician and Llandovery specimens referred to *Pygodus*, and it is possible that the two groups are homeomorphic.

Genus ***SAGITTODONTUS*** Rhodes, 1953

TYPE SPECIES. *Sagittodontus robustus* Rhodes, 1953.

Sagittodontus edentatus (Branson & Branson)

Plate 7, figs 1–3

1947 *Trichonodella*? *edentata* Branson & Branson: 552, pl. 81, fig. 28; pl. 82, figs 40, 44, 48.
1947 *Trichonodella brassfieldensis* Branson & Branson (*partim*): 551 pl. 82, fig. 49 only.

1947 *Trichonodella carinata* Branson & Branson (*partim*): 552, pl. 82, figs 27, 34 only.
1967 *Trichonodella? edentata* Branson & Branson; Rexroad: 55, pl. 3, figs 31–34.
1968 *Trichonodella? edentata* Branson & Branson; Nicoll & Rexroad: 63, pl. 4, figs 16–18.
1970 *Sagittodontus edentatus* (Branson & Branson) Pollock, Rexroad & Nicoll: 759, pl. 112, figs 21–23.

MATERIAL. 45 specimens: figured (X.662), (X.663), (X.664).

OCCURRENCE. Idwian to Telychian.

DESCRIPTION. The stout cusp is erect or slightly posteriorly curved, with sharp posterior and lateral edges. The transverse section of the cusp is triangular with the outer lateral face broader than the inner lateral face. The base of the cusp is expanded and gives rise to three processes, two lateral and one posterior, continuous with the sharp edges of the cusp. The inner lateral process is directed aborally as an anticusp-like extension of the cusp and does not usually support denticles. The outer lateral process is directed aborally and outwards and commonly bears short denticles, fused nearly to their apices. The posterior bar is directed a little downwards, and commonly bears low, fused denticles, although these may be absent. The cusp is deeply excavated and the cavity extends as deep grooves beneath the processes.

REMARKS. As suggested by Pollock, Rexroad & Nicoll (1970 : 752), *S. edentatus* appears to be a transitional form in the evolution of *Exochognathus* from *Sagittodontus*. Poorly denticulate specimens resemble *S. robustus* Rhodes (1953 : 311, pl. 21, figs 141, 142) and those with well-developed denticulation of the processes are close to *E. brassfieldensis*.

Genus ***SPATHOGNATHODUS*** Branson & Mehl, 1941

TYPE SPECIES. *Spathodus primus* Branson & Mehl, 1933.

Spathognathodus abruptus sp. nov.

Plate 4, figs 6, 7

DERIVATION OF NAME. Latin, steep, with reference to the sudden decrease in the height of the denticles near the posterior tip of the blade.

DIAGNOSIS. *Spathognathodus* Branson & Mehl with a blade that is deflected inwards in the posterior quarter of its length. A small number of denticles at the posterior end of the blade are considerably shorter than the remainder. The flared basal cavity extends to the posterior tip of the unit.

HOLOTYPE. Specimen (X.574).

MATERIAL. 29 specimens: figured (X.574), (X.575).

TYPE LOCALITY AND HORIZON. Venusbank Formation of Hope Quarry, sample H.Q.3.

OCCURRENCE. Idwian and Fronian.

Description. Along the greater part of its length the blade consists of a row of 11 to 13 denticles, of subequal size and laterally compressed. The posterior denticle of this row is commonly slightly larger than the others and the three or four denticles anterior to it are compressed antero-posteriorly. Beyond the main denticle, the posterior part of the blade is deflected inwards by up to 30° and supports three or four considerably smaller denticles. The basal cavity is flanked by widely flaring lips from the posterior tip to almost the midlength of the unit, and continues as a groove to the anterior tip. The cavity is deepest and most widely flared beneath the point of deflection of the blade. The flaring is stronger on the outer side of the unit and the oral surface may be wrinkled into low ridges on the outer anterior portion.

Remarks. There are close similarities to *Spathognathodus manitoulinensis* Pollock, Rexroad & Nicoll (1970 : 761–762, pl. 111, figs 17–19), which also displays a deflected blade and abrupt lowering of the denticles over a flared basal cavity. In *S. manitoulinensis*, however, the deflection is typically about 60°, and a greater number of denticles are present on the posterior part of the blade, which extends beyond the limit of the flared cavity. The flaring of the cavity is almost totally restricted to the outer side, where the outline approaches semicircular. The similarities between the two species suggest a relationship, and the differences may be due to facies control, geographical isolation or successional isolation.

A single specimen (X.576) of Fronian age is identified as *Spathognathodus* cf. *S. abruptus* (Pl. 4, fig. 8). The posterior end of the blade is characterized by two low denticles, which curve only slightly away from the line of the rest of the blade. The lips of the cavity, although broken, appear to be more symmetrically flared than is typical for *S. abruptus*. It is possible that this specimen is a transitional form in the evolution of *S. ranuliformis* from *S. abruptus*.

Spathognathodus gulletensis sp. nov.

Plate 4, figs 9–12

1965 *Spathognathodus* cf. *celloni* Walliser; Brooks & Druce: 377, pl. 12, figs 2, 3.

Derivation of name. After Gullet Quarry in the Malvern Hills, where this species is particularly abundant.

Diagnosis. *Spathognathodus* Branson & Mehl with fused denticles that are lower in the posterior one-third of the unit. The basal cavity is situated at, or slightly posterior to, midlength and has asymmetrically flared lips, which in outline are either rounded or posteriorly extended into an arrow shape.

Holotype. Specimen (X.577).

Material. 323 specimens: figured (X.577), (X.578), S.1.37, (X.580).

Type locality and horizon. The Wych Formation of Gullet Quarry, sample Gullet 2.

Occurrence. A single specimen from C_{3-4}, abundant in C_5 (Telychian).

Description. The blade is straight and bears a row of laterally compressed, sharp denticles, fused nearly to their apices. The denticles vary in number from 13 to 18, but most specimens possess 15 or 16. The posterior four to seven denticles are lower than the remainder, which are of subequal height. There is often a single, slightly larger denticle immediately anterior to the low posterior denticles. One or two denticles at the anterior end of the blade may be somewhat broader than the others. The basal cavity is situated at, or slightly posterior to, midlength of the unit and has flared lips. The outline of the cavity is asymmetrical and may be subcircular or somewhat extended posteriorly to give an arrow shape. The cavity continues as a groove under the blade to the anterior and posterior tips.

Remarks. There is a general morphological resemblance to *S. hassi*, from which *S. gulletensis* appears to have evolved by a decrease in the size of the apical denticle and an alteration in the outline of the basal cavity. There is also some similarity to *Spathognathodus primus* (Branson & Mehl), which differs in possessing very tall anterior denticles.

Spathognathodus hassi Pollock, Rexroad & Nicoll

Plate 4, figs 2, 3

1967 *Spathognathodus* cf. *S. oldhamensis* Rexroad: pl. 3, fig. 3.
1970 *Spathognathodus hassi* Pollock, Rexroad & Nicoll: 760, pl. 111, figs 8–12.

Material. 35 specimens: figured (X.624), (X.625).

Occurrence. Idwian and Fronian.

Description. The blade is straight or slightly bowed and bears a row of tall, laterally compressed denticles, fused nearly to their apices. The blade is commonly a little thickened below the denticle row. The denticle above the basal cavity, a little posterior of centre, is larger than the others. The denticles to the posterior of the apical denticle are shorter than those to the anterior. The basal cavity is flanked by widely flared lips, which are rounded and a little asymmetrical in outline.

Remarks. A single specimen of Fronian age has a poorly developed apical denticle and a somewhat elongated cavity, and appears to be transitional towards *S. gulletensis* sp. nov. The relationship of *S. hassi* to *S. oldhamensis* is discussed under that species.

Spathognathodus inclinatus (Rhodes)

Plate 4, figs 15, 16

1953 *Prioniodella inclinata* Rhodes: 324, pl. 23, figs 233–235.
1957 *Spathognathodus inclinatus* (Rhodes) Walliser: 47, pl. 1, figs 16–20.
1960 *Spathognathodus* n. sp. Walliser: 35, pl. 8, fig. 7.
1964 *Spathognathodus inclinatus inclinatus* (Rhodes) Walliser: 76, pl. 8, fig. 6; pl. 19, figs 6–21.
1966 *Spathognathodus inclinatus* (Rhodes) Barnett *et al.*: pl. 58, fig. 23.
1966 *Spathognathodus inclinatus inclinatus* (Rhodes) Philip: 450, pl. 1, figs 30, 31, 34, 35, 37–39.
1969 *Hindeodella excavata* (Branson & Mehl) Jeppson (*partim*): 18, text-figs 1G, 3A.

Material. 111 specimens: figured (X.627), (X.628).

Occurrence. Fronian and Telychian.

Description. The blade is straight or arched and is commonly laterally thickened below the denticle row. The denticles are closely packed, often partially fused, and inclined posteriorly. The denticles in the central portion of the blade are a little larger than those at the ends, and some specimens possess a single denticle that is markedly larger than the others. Beneath the largest denticle the basal cavity is expanded laterally and is flanked by flared lips. The cavity continues as a groove on the aboral surface of the blade to the anterior and posterior tips.

Remarks. Some specimens, which possess an apical denticle and show less thickening of the blade than is typical, resemble *Ozarkodina* n. sp. A and *Ozarkodina* n. sp. B of Pollock, Rexroad & Nicoll (1970 : 757, pl. 113, figs 5–11). The phylogenetic relationships of this group of species are obscure, and it is possible that the Llandovery specimens may be homeomorphs of the *Spathognathodus inclinatus* group from younger Silurian strata.

Spathognathodus oldhamensis Rexroad

Plate 4, fig. 1

1967 *Spathognathodus oldhamensis* Rexroad: 49, pl. 3, figs 1, 2.
1970 *Spathognathodus oldhamensis* Rexroad; Pollock, Rexroad & Nicoll: 762, pl. 111, figs 13–16.

Material. 51 specimens: figured (X.626).

Occurrence. Idwian and Fronian.

Description. The blade is straight or slightly bowed and bears a row of laterally compressed denticles. The denticles at the anterior end are inclined slightly anteriorly and fused nearly to their apices. The denticles immediately posterior of centre are completely fused and are commonly succeeded posteriorly by a very small denticle. The denticles at the posterior end are inclined a little posteriorly and are partially to almost completely fused. The shallow basal cavity is situated somewhat posterior of centre and has very widely flared lips. The outline of the asymmetrical cavity is a laterally elongated ellipse.

Remarks. As remarked by Pollock, Rexroad & Nicoll (1970 : 761), there is a close relationship to *S. hassi*, which differs in possessing an apical denticle and in the more uniform spacing of the denticles. The two species have similar stratigraphic ranges and probably evolved from a common ancestor.

Spathognathodus polinclinatus Nicoll & Rexroad

Plate 4, fig. 13

1968 *Spathognathodus polinclinatus* Nicoll & Rexroad: 60, pl. 2, figs 19, 20.

Material. 13 specimens: figured, S.3.8.

Occurrence. Telychian (C_5).

Description. The blade is straight and bears a row of erect, laterally compressed denticles. The denticles are of subequal size and are fused nearly to their apices. Beneath the posterior half of the blade is a shallow basal cavity, flanked by very narrow lips. The cavity continues as a groove under the anterior half of the blade.

Spathognathodus ranuliformis Walliser

Plate 4, fig. 14

1964 *Spathognathodus ranuliformis* Walliser: 82, pl. 6, fig. 9; pl. 22, figs 5–7.
1968 *Spathognathodus ranuliformis* Walliser; Nicoll & Rexroad: 60, pl. 2, figs 10, 11.
1969 *Spathognathodus ranuliformis* Walliser; Drygant: 50, pl. 1, fig. 4.

Material. 46 specimens: figured (X.630).

Occurrence. Telychian to early Wenlock.

Description. The blade is almost straight, but curves slightly inwards at the posterior end. The denticles are erect and fused nearly to their tips. The posterior end of the blade commonly comprises a single larger denticle, succeeded posteriorly by one or two smaller denticles. The cavity is flanked by extensively flared lips at the posterior end and continues as a groove to the anterior tip of the blade. The flared cavity is subcircular in outline and extends beyond the posterior limit of the blade.

Remarks. Two specimens from C_{3-4} are identified as *Spathognathodus* cf. *S. ranuliformis*. The cavity of these specimens is less flared than is typical and the blade extends to the posterior tip of the unit. These specimens appear to be transitional from *S. abruptus*.

Spathognathodus sp. A nov.

Plate 4, fig. 4

Material. 14 specimens: figured, S.3.9.

Occurrence. Fronian/Telychian.

Description. The straight blade bears 15 to 18 denticles of subequal height. The denticles in the central portion are completely fused, those at each end partially fused. The basal cavity is situated posterior of midlength and is enclosed by asymmetrical, widely-flared lips, which have a rounded to somewhat arrow-shaped outline. The cavity extends as a narrow groove to the tips of the blade.

Remarks. The denticulation is similar to that of *S. oldhamensis*, from which this species may be descended. The outline of the basal cavity is similar to that of *S. gulletensis*.

Spathognathodus sp. B nov.

Plate 4, fig. 5

Material. 6 specimens: figured (X.629).

Occurrence. Fronian/Telychian.

Description. The straight blade bears 13 to 16 denticles that decrease in height posteriorly. The denticles are fused nearly to their sharp apices, and a few to the posterior of midlength may be more completely fused. Alternatively, a few much broader denticles may be present in this position. The flaring of the basal cavity begins slightly anterior of midlength and extends nearly to the posterior tip. The outline of the almost symmetrical cavity is an antero-posteriorly elongated ellipse. The cavity extends as a groove to the tips of the blade.

Remarks. The relationships to other species of *Spathognathodus* are obscure. The denticulation is somewhat similar to that of *S. oldhamensis* and *S.* sp. nov. A, and this species possibly evolved from that lineage. There is a morphological resemblance to some of the specimens of *S. inclinatus inflatus*, illustrated by Walliser (1964 : pl. 19, fig. 24).

Genus ***SYNPRIONIODINA*** Ulrich & Bassler, 1926

Type species. *Synprioniodina alternata* Ulrich & Bassler, 1926.

Synprioniodina bicurvata (Branson & Mehl)

Plate 5, fig. 28

1933 *Prioniodus bicurvatus* Branson & Mehl: 44, pl. 3, figs 9–12.
1956 *Prioniodina tropa* (Stauffer) Ziegler: 104, pl. 6, fig. 29; pl. 7, fig. 29.
1958 *Prioniodina bicurvata* (Branson & Mehl) Bischoff & Sannemann: 102, pl. 15, figs 6, 12.
1960 *Prioniodina bicurvata pronoides* Walliser: 33, pl. 8, figs 8–10.
1960 *Prioniodina bicurvata pronoides* Walliser; Ziegler: 193, pl. 15, figs 8, 9.
?1964 *Prioniodina bicurvata* (Branson & Mehl); Serpagli & Greco: 207, pl. 37, fig. 11.
1964 *Neoprioniodus bicurvatus* (Branson & Mehl) Walliser: 46, pl. 29, figs 27–30, 31–33?; text-fig. 5d.
1965 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 105, pl. 9, figs 13, 18, 20.
1966 *Neoprioniodus bicurvatus* (Branson & Mehl); Barnett *et al.*: pl. 58, fig. 22.
1966 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 446, pl. 3, figs 12–16.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1C, 2C.
1969 *Neoprioniodus bicurvatus* (Branson & Mehl); Philip: 292, pl. 17, fig. 15.
1970 *Synprioniodina bicurvata* (Branson & Mehl) Pollock, Rexroad & Nicoll: 762, pl. 114, figs 16, 17.

Material. 10 specimens: figured (X.661).

Occurrence. Idwian to Telychian.

Description. The cusp is straight, with sharp anterior and posterior edges. The posterior bar is curved strongly downwards and may be bowed inwards. The denticles of the posterior bar are of subequal size and may be discrete or closely packed.

The anterior bar forms a sharply pointed downward extension of the cusp, is very short and may or may not bear a few small, fused denticles. The basal cavity is slightly flared beneath the cusp, but narrows rapidly below the posterior bar.

Synprioniodina silurica Walliser

Plate 5, fig. 27

1964 *Synprioniodina silurica* Walliser: 88, pl. 6, fig. 12; pl. 8, fig. 18; pl. 29, figs 38–41; pl. 30, figs 1–4, 6.
1968 *Synprioniodina silurica* Walliser; Nicoll & Rexroad: 61, pl. 4, fig. 10.
1970 *Synprioniodina silurica* Walliser; Pollock, Rexroad & Nicoll: 762, pl. 114, fig. 15.

MATERIAL. 18 specimens: figured (X.660).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is stout and straight, with sharp anterior and posterior edges. The posterior bar is deep, strongly downcurved and bears several discrete denticles. The anterior bar is usually very much shorter and bears only two or three denticles. The cavity is widened and flared beneath the cusp and is slightly extended posteriorly.

REMARKS. Most of these specimens are broken, and the range of variation cannot be determined. The sharp anterior and posterior margins of the cusp indicate a closer similarity to the specimens described from Europe by Walliser (1964) than to those described from North America by Nicoll & Rexroad (1968).

Genus ***TRICHONODELLA*** Branson & Mehl, 1948

TYPE SPECIES. *Trichognathus prima* Branson & Mehl, 1933.

Trichonodella asymmetrica Nicoll & Rexroad

Plate 7, fig. 17

1968 *Trichonodella asymmetrica* Nicoll & Rexroad: 62, pl. 4, fig. 7.

MATERIAL. 9 specimens: figured (X.680).

OCCURRENCE. Fronian and Telychian.

DESCRIPTION. The cusp is inclined posteriorly and twisted. The transverse section of the cusp is subtriangular. The denticulate lateral processes are deep and one is considerably longer than the other. The shorter process bears about four comparatively tall, discrete denticles. The longer process bears about six shorter, discrete denticles. The basal cavity is shallow beneath the cusp and is slightly extended posteriorly.

Trichonodella excavata (Branson & Mehl)

Plate 7, fig. 20

1933 *Trichognathus excavata* Branson & Mehl: 51, pl. 3, figs 35, 36.
1953 *Trichonodella aborflexa* Rhodes: 312, pl. 23, figs 231, 241, 242.
1957 *Trichonodella excavata* (Branson & Mehl) Walliser: 48, pl. 3, figs 3, 4, 6–8.
1958 *Trichonodella excavata* (Branson & Mehl); Bischoff & Sannemann: 109, pl. 15, figs 16, 18.
1962 *Trichonodella excavata* (Branson & Mehl); Ethington & Furnish: 1287, pl. 173, fig. 8.
1964 *Trichonodella excavata* (Branson & Mehl); Walliser: 89, pl. 8, fig. 2; pl. 31, figs 26, 27.
1966 *Trichonodella excavata* (Branson & Mehl); Barnett *et al.*: pl. 58, fig. 14.
1968 *Trichonodella excavata* (Branson & Mehl); Nicoll & Rexroad: 63, pl. 4, fig. 2.
1969 *Hindeodella excavata* (Branson & Mehl); Jeppsson (*partim*): 18, text-figs 1L, 3F.

MATERIAL. 49 specimens: figured (X.685).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The cusp is tall, slender and posteriorly inclined. The lateral processes bear closely packed denticles and diverge at an angle of 120°–160°, together forming a symmetrical arch. The basal cavity beneath the cusp is shallow, but is considerably expanded posteriorly, forming a wide groove which extends upwards for about a quarter of the length of the cusp. The cavity continues as a shallow groove on the aboral surface of the processes.

REMARKS. A few specimens show a degree of asymmetry and flexing of the processes, indicative of transition towards *Plectospathodus extensus*.

Trichonodella? expansa Nicoll & Rexroad

Plate 7, fig. 14

1968 *Trichonodella*? *expansa* Nicoll & Rexroad: 64, pl. 4, figs 19–22.

MATERIAL. 36 specimens: figured (X.679).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The tall, stout cusp is posteriorly inclined and a little twisted. The transverse section of the cusp varies from square to triangular. The base is expanded and gives rise to three or four variably developed processes, which are also expanded to give a platform. The two lateral processes and the posterior process are usually well-developed and denticulate. The posterior process is commonly the longest. A poorly developed anterior process may be present. A shallow cavity, usually containing basal material, is excavated on the aboral surface.

REMARKS. Specimens from older strata display a less expanded base and a squarer cusp than those from younger strata. There appears to be a gradual increase in the expansion of the base with time.

The generic position of this species is very questionable. Nicoll & Rexroad (1968) suggested that it evolved from *Sagittodontus edentatus*, but such a phylogenetic relationship is not apparent in this material, There is no evidence for any relationship with representatives of the genus *Trichonodella*, but the name assigned by Nicoll & Rexroad is retained until the generic position has been satisfactorily resolved.

Trichonodella inconstans Walliser

Plate 7, fig. 16

1957 *Trichonodella inconstans* Walliser: 50, pl. 3, figs 10–17.
1958 *Trichonodella inconstans* Walliser; Bischoff & Sannemann: 109, pl. 15, figs 20, 21.
1960 *Trichonodella inconstans* Walliser; Ziegler: 197, pl. 14, figs 14, 17.
1962 *Trichonodella inconstans* Walliser; Ethington & Furnish: 1287, pl. 173, fig. 7.
1964 *Trichonodella inconstans* Walliser; Walliser: 90, pl. 8, fig. 8; pl. 30, figs 10–12.
1965 *Trichonodella inconstans* Walliser; Philip (*partim*): 112, pl. 9, fig. 15 only.
1965 *Trichonodella* aff. *T. inconstans* Walliser; Brooks & Druce: 378, pl. 12, fig. 4.
1966 *Trichonodella inconstans* Walliser; Philip: 451, pl. 3, fig. 23; pl. 4, figs 21, 23, 27, 30.
1967 *Trichonodella* cf. *T. inconstans* Walliser; Rexroad: 54, pl. 3, fig. 19.
1968 *Trichonodella inconstans* Walliser; Nicoll & Rexroad: 64, pl. 4, fig. 1.
1969 *Trichonodella inconstans* Walliser; Philip: 295, pl. 18, figs 9, 12, 14, 15.
1970 *Trichonodella inconstans* Walliser; Pollock, Rexroad & Nicoll: 762, pl. 113, figs 26, 27.

MATERIAL. 99 specimens: figured (X.684).

OCCURRENCE. Idwian to early Wenlock.

DESCRIPTION. The posteriorly inclined cusp is circular in transverse section. The lateral processes are more or less symmetrical and bear widely spaced denticles. The basal cavity is wide and deep beneath the cusp and continues as a groove under the processes.

REMARKS. The wide range of variation remarked upon by previous authors is apparent in this material. Many specimens are included that are transitional to *Lonchodina greilingi* and it is possible that Pollock, Rexroad & Nicoll (1970 : 763) were correct in considering that these two species should be grouped together.

Trichonodella symmetrica (Branson & Mehl)

Plate 7, figs 15, 18, 19

1933 *Trichognathus symmetrica* Branson & Mehl: 50, pl. 3, figs 33, 34.
1953 *Trichonodella symmetrica* (Branson & Mehl); Rhodes (*partim*): 315, pl. 23, fig. 246 only.
1964 *Trichonodella symmetrica* (Branson & Mehl); Walliser: 90, pl. 9, fig. 11; pl. 31, figs 28–30.
1965 *Trichonodella symmetrica* (Branson & Mehl); Philip: 112, pl. 9, figs 19, 21.
1968 *Trichonodella symmetrica* (Branson & Mehl); Igo & Koike: 19, pl. 3, figs 10, 11.
1969 *Hindeodella confluens* Branson & Mehl; Jeppsson (*partim*): 15, text-figs 1F, 2F.
1969 *Trichonodella symmetrica* (Branson & Mehl); Philip: 295, pl. 18, fig. 24.
1970 *Trichonodella symmetrica* (Branson & Mehl); Pollock, Rexroad & Nicoll: 763, pl. 113, figs 22–24.

MATERIAL. 53 specimens: figured (X.681), (X.682), (X 683).

OCCURRENCE. Idwian to early Wenlock.

Description. The erect cusp is triangular to subtriangular in transverse section. The posterior edge of the cusp is sharp, the anterior face is flat or gently convex. The lateral processes are symmetrical and bear closely packed denticles. A shallow cavity is excavated beneath the cusp, but is not conspicuously extended posteriorly or laterally.

gen. et sp. indet. A

Plate 8, fig. 18

Material. 1 specimen: figured (X.693).

Occurrence. C_{3-4}.

Description. The unit consists of a long bar, which does not appear to be broken at either end. In lateral view, the aboral edge of the bar is gently projected aborally near one end to form a slight lip. The bar bears 17 discrete denticles of unequal size, without a distinguishable cusp. The denticles are somewhat laterally compressed and are elliptical in transverse section. The aboral surface of the bar is grooved along its entire length, the groove being widest and deepest in the area of the aborally projecting lip.

gen. et sp. indet. B

Plate 5, fig. 29

Material. 1 specimen: figured (X.694).

Occurrence. C_{3-4}.

Description. The unit consists of a straight, denticulate bar and a short, denticulate lateral process. The main bar bears a large denticle at one end, which may be taken as the cusp. The cusp is laterally compressed with sharp anterior and posterior edges and a sharp tip. Anterior to the cusp are seven sharp, laterally compressed denticles. The two denticles at the anterior end of the bar are short and almost totally fused. The remaining five denticles are nearly as tall as the cusp and fused only near their bases. The lateral process arises adjacent to the denticle immediately anterior to the cusp and points laterally and slightly anteriorly, making an angle of about 75° with the blade. The process bears two short, partially fused denticles that are compressed in the plane of the process. The entire aboral surface is excavated by a shallow groove, which is filled with basal material.

VII. CONCLUSIONS

Samples collected from Llandovery and early Wenlock strata of the Welsh Borderland yielded well-preserved and diversified conodont faunas. The collecting techniques employed in this investigation were largely those of reconnaissance and only well-documented, major exposures were visited in the separate areas. There is strong evidence that conodont faunal assemblages changed considerably through the period studied, and four assemblage zones can be broadly recognized in the Welsh Borderland. The potential value of conodonts in refined stratigraphic correlation of the Llandovery has, therefore, been established and it is now necessary to undertake detailed sampling in each area where valuable conodont faunas are known to occur. When completed, this should enable clear definition of zonal boundaries. In addition, it is probable that phylogenetic lineages for important genera such as *Spathognathodus* and *Icriodella* will be established by studies of successional populations, and these will form an important tool for local and intercontinental correlation. Before detailed correlations can be achieved, it will be necessary to add to the knowledge of the effects of facies control and faunal provincialism on the distribution of Llandovery conodonts.

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X. APPENDIX

a. List of sample localities

District	*Sample No.*	*Grid Ref.*
Llandovery	LL 1a	SN/729308
	LL 2a, b	SN/753309
	LL 3a	SN/744289
	LL 4a	SN/747289
	LL 5a–c	SN/757324
	LL 6a	SN/753319
	LL 7a	SN/757312
	LL 8a	SN/758311
	LL 9a, b	SN/759311
	LL 10a	SN/761309
	LL 11a	SN/759309
	LL 12a	SN/775328
	LL 13a	SN/762325
	LL 14a	SN/775326
	LL 15a	SN/775325
	LL 16a	SN/775324
	LL 17a	SN/775323
Llandeilo	Sawdde Gorge	SN/715260
Montgomeryshire	Graig-wen Quarry	SJ/099091
	Gelli Farm 1–6	SJ/236193
	Welshpool 1–3	SJ/219128
Breidden Hills	Middletown	SJ/301128
	Buttington 1–3	SJ/265100
Hope Valley	H.Q.1–6	SJ/355021
	H.V.1	SJ/355021
	H.V.2	SJ/357022
	H.V.3	SJ/358022
	H.V.4	SJ/360022
	H.V.5	SJ/361022
	H.V.6	SJ/364025
	H.B.1, 2	SJ/364022
	Minsterley Lane	SJ/380049
Long Mynd	Hillend Farm	SO/394876
	Plowden B1	SO/391873
	Plowden 1–8	SO/396877
	Norbury 1–3	SO/364928
	Norbury A1, A2	SO/359928
	New House, Marshbrook	SO/434898
	Onny River	SO/426853
Wenlock Edge	Ticklerton Brook	SO/482909
	Ticklerton 1–3	SO/481901
	Gilberries	SO/512936
	Sheinton 1	SJ/610032
	Sheinton 2	SJ/612031
	Domas	SJ/594006
	Dingle	SJ/633070
Malvern Hills	Gullet 1–4	SO/761381
	MB 68/16, 16a–c (Hollybush)	SO/760371
	West Malvern 1, 2	SO/765459
	Cowleigh Park 1, 2	SO/760468
Woolhope	Haugh Wood 2–4	SO/589358
	Woolhope 1	SO/612353
Tortworth	Tortworth 1–3	ST/706943
	Tortworth 4	ST/688957
	Damery Beds	ST/706934

b. Sample weights and conodont abundances

Samples that did not respond to chemical treatment are not included.

Sample No.	*Weight (kg)*	*Conodonts*	*Conodonts/ kg*
LL 4a	1·50	0	0
LL 8a	1·75	0	0
LL 10a	1·00	0	0
LL 17a	3·25	0	0
Sawdde Gorge	2·50	0	0
Graig-wen Quarry	1·25	0	0
Gelli Farm 1	1·50	0	0
Gelli Farm 2	1·25	83	66
Gelli Farm 3	3·50	72	20
Gelli Farm 4	2·00	8	4
Gelli Farm 5	2·25	2	1
Gelli Farm 6	1·75	1	1
Welshpool 1	1·50	27	18
Welshpool 2	1·00	0	0
Welshpool 3	1·25	0	0
Middletown	1·00	0	0
H.Q.1	14·00	108	8
H.Q.2	1·00	0	0
H.Q.3	14·00	291	21
H.Q.4	2·00	0	0
H.Q.5	1·00	4	4
H.Q.6	1·25	32	26
H.V.1	1·50	0	0
H.V.2	1·50	2	1
H.V.3	2·00	285	142
H.V.4	5·00	748	150
H.V.5	2·00	15	7
H.V.6	1·00	0	0
H.B.1	1·00	4	4
H.B.2	5·00	116	23
Minsterley Lane	3·50	163	46
Plowden B1	2·50	13	5
Plowden 1	25·00	424	17
Plowden 2	13·50	215	16
Plowden 3	17·00	245	14
Plowden 4	7·00	43	6
Plowden 5	11·00	28	3
Plowden 6	9·50	88	9
Plowden 7	9·50	65	7
Plowden 8	9·50	63	7
Norbury 1	1·00	70	70
Norbury 2	1·25	6	5
Norbury 3	3·50	89	25
Norbury A1	2·50	4	2
Norbury A2	1·00	0	0
New House, Marshbrook	3·00	391	130
Onny River	1·00	0	0
Ticklerton Brook	1·25	692	550
Ticklerton 1	5·00	544	109
Ticklerton 2	2·00	116	58
Ticklerton 3	4·50	531	118
Gilberries	1·00	1	1
Sheinton 1	1·25	0	0
Sheinton 2	6·00	519	87
Domas	1·75	0	0
Dingle Grit	1·50	18	12
Dingle Conglom.	2·50	13	5
Gullet 1	9·00	50	6
Gullet 2	8·50	645	76
Gullet 2A	2·25	175	78
Gullet 3	6·00	78	13
Gullet 4	5·00	2913	583
MB 68/16a	2·00	29	14
MB 68/16b	2·00	137	68
MB 68/16c	2·00	3	2
MB 68/16	2·00	30	15
West Malvern 1	6·00	146	24
West Malvern 2	2·00	35	17
Cowleigh Park 1	3·00	1011	337
Cowleigh Park 2	2·25	27	12
Haugh Wood 2	2·25	0	0
Haugh Wood 3	6·00	125	21
Haugh Wood 4	1·50	0	0
Woolhope 1	3·00	118	39
Tortworth 1	2·00	0	0
Tortworth 2	1·25	0	0
Tortworth 3	1·00	0	0
Tortworth 4	5·25	11	2
Damery Beds	—	52	—
T-R-A	—	9	—
M-G-C	—	8	—

c. Register of figured specimens

Slide No.	*Conodont*	*Sample No.*
X.561	*Icriodella deflecta* sp. nov. holotype	H.Q.3
S.1.2	*Icriodella deflecta* sp. nov.	H.Q.1
X.562	*Icriodella deflecta* sp. nov.	H.Q.3
S.1.4	*Icriodella deflecta* sp. nov.	H.Q.3
X.563	*Icriodella inconstans* sp. nov. holotype	Gullet 2
X.564	*Icriodella inconstans* sp. nov.	Gullet 2
S.1.9	*Icriodella inconstans* sp. nov.	Gullet 2
X.565	*Icriodella inconstans* sp. nov.	Gullet 4
X.566	*Icriodella inconstans* sp. nov.	Gullet 4
X.567	*Icriodella malvernensis* sp. nov. holotype	West Malvern 1
X.568	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.569	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.570	*Icriodella malvernensis* sp. nov.	West Malvern 1
X.571	*Icriodella* cf. *I. malvernensis* sp. nov.	Sheinton 2
X.572	*Amorphognathus tenuis* sp. nov. holotype	Plowden 3
X.573	*Amorphognathus tenuis* sp. nov.	New House, Marshbrook
X.574	*Spathognathodus abruptus* sp. nov. holotype	H.Q.3
X.575	*Spathognathodus abruptus* sp. nov.	Plowden 7
X.576	*Spathognathodus* cf. *S. abruptus* sp. nov.	Minsterley Lane
X.577	*Spathognathodus gulletensis* sp. nov. holotype	Gullet 2
X.578	*Spathognathodus gulletensis* sp. nov.	Gullet 2
S.1.37	*Spathognathodus gulletensis* sp. nov.	Gullet 2
X.580	*Spathognathodus gulletensis* sp. nov.	West Malvern 1
X.581	*Ozarkodina alisonae* sp. nov. holotype	Gullet 2
X.582	*Ozarkodina alisonae* sp. nov.	Gullet 2
X.583	*Diadelognathus nicolli* sp. nov. holotype	Ticklerton 1
X.584	*Diadelognathus nicolli* sp. nov.	Ticklerton 1
X.585	*Icriodella discreta*	Gelli Farm 3
X.586	*Icriodella discreta*	Gelli Farm 3
X.587	*Icriodella discreta*	Gelli Farm 3
X.588	*Icriodina irregularis*	H.Q.3
X.589	*Icriodina* sp.	H.V.4
X.590	*Hadrognathus staurognathoides*	Sheinton 2
X.591	*Hadrognathus staurognathoides*	Sheinton 2
X.592	*Hadrognathus staurognathoides*	Ticklerton 1
X.593	*Apsidognathus tuberculatus*	Gullet 4
X.594	*Apsidognathus tuberculatus*	Gullet 4
X.595	*Aulacognathus kuehni*	Gullet 1
X.596	*Astropentagnathus irregularis*	MB 68/16b
X.597	*Neospathognathodus celloni*	Gullet 4
X.598	*Neospathognathodus celloni*	Gullet 4
X.599	*Neospathognathodus celloni*	MB 68/16b
X.600	*Neospathognathodus celloni*	MB 68/16b
X.601	*Neospathognathodus pennatus*	Gullet 4
X.602	*Neospathognathodus pennatus*	Cowleigh Park 1
X.603	*Neospathognathodus*? sp.	H.Q.3
X.604	*Neospathognathodus bullatus*	Gullet 4
X.605	*Pterospathodus amorphognathoides*	Cowleigh Park 1
X.606	*Pterospathodus amorphognathoides*	Cowleigh Park 1
X.607	*Pterospathodus amorphognathoides*	Ticklerton 2
X.608	*Astrognathus tetractis*	Gullet 4

Slide No.	*Conodont*	*Sample No.*
X.609	*Pygodus? lyra*	Gullet 4
S.2.64	*Carniodus carinthiacus*	Cowleigh Park 1
S.2.65	*Carniodus carinthiacus*	Cowleigh Park 1
X.610	*Carniodus carinthiacus*	Cowleigh Park 1
X.611	*Carniodus carnicus*	Cowleigh Park 1
X.612	*Carniodus carnulus*	Cowleigh Park 1
X.613	*Carniodus carnulus*	Cowleigh Park 1
X.614	*Carniodus carnulus* aberrant form	Cowleigh Park 1
X.615	*Carniodus carnus*	Cowleigh Park 1
S.2.72	*Carniodus carnus*	Cowleigh Park 1
X.616	*Carniodus* cf. *C. carnus*	New House, Marshbrook
X.617	*Carniodus* cf. *C. eocarnicus*	New House, Marshbrook
X.618	*Aphelognathus siluricus*	Plowden 2
X.619	*Ambalodus anapetus*	New House, Marshbrook
X.620	*Ambalodus* sp.	New House, Marshbrook
X.621	*Ambalodus triangularis*	Ticklerton Brook
X.622	*Ambalodus galerus*	Gullet 4
X.623	*Ambalodus galerus*	Gullet 4
X.624	*Spathognathodus hassi*	Plowden 1
X.625	*Spathognathodus hassi*	New House, Marshbrook
X.626	*Spathognathodus oldhamensis*	H.Q.1
X.627	*Spathognathodus inclinatus*	Sheinton 2
X.628	*Spathognathodus inclinatus*	Gullet 2
S.3.8	*Spathognathodus polinclinatus*	MB 68/16b
S.3.9	*Spathognathodus* sp. nov. A	Minsterley Lane
X.629	*Spathognathodus* sp. nov. B	Sheinton 2
X.630	*Spathognathodus ranuliformis*	Ticklerton 2
S.3.12	*Ozarkodina adiutricis*	MB 68/16b
X.631	*Ozarkodina adiutricis*	MB 68/16b
X.632	*Ozarkodina* cf. *O. edithae*	MB 68/16b
X.633	*Ozarkodina gaertneri*	Ticklerton 1
X.634	*Ozarkodina gaertneri*	Cowleigh Park 1
X.635	*Ozarkodina hanoverensis*	West Malvern 1
X.636	*Ozarkodina media*	Ticklerton Brook
X.637	*Ozarkodina typica*	H.V.4
X.638	*Ozarkodina typica*	Minsterley Lane
X.639	*Ozarkodina typica*	New House, Marshbrook
X.640	*Distomodus? extrorsus*	H.Q.3
X.641	*Distomodus? egregius*	H.Q.3
X.642	*Distomodus? egregius*	Sheinton 2
X.643	*Distomodus? egregius*	Ticklerton 1
S.3.30	*Distomodus* sp. nov.	Sheinton 2
X.644	*Distomodus kentuckyensis*	H.Q.3
X.645	*Distomodus kentuckyensis*	H.Q.3
X.646	*Distomodus kentuckyensis*	Plowden 1
X.647	*Distomodus kentuckyensis*	Sheinton 2
X.648	*Distomodus kentuckyensis*	Sheinton 2
X.649	*Gothodus?* sp. nov.	New House, Marshbrook
X.650	*Distomodus triangularis tenuirameus*	Gullet 4
X.651	*Distomodus triangularis triangularis*	Cowleigh Park 1
X.652	*Neoprioniodus costatus paucidentatus*	H.Q.3
X.653	*Neoprioniodus costatus paucidentatus*	Gullet 4

Slide No.	*Conodont*	*Sample No.*
X.654	*Neoprioniodus costatus costatus*	Ticklerton 1
X.655	*Neoprioniodus excavatus*	Ticklerton 3
X.656	*Neoprioniodus latidentatus*	Sheinton 2
X.657	*Neoprioniodus multiformis*	H.V.3
X.658	*Neoprioniodus planus*	Sheinton 2
X.659	*Neoprioniodus subcarnus*	Cowleigh Park 1
X.660	*Synprioniodina silurica*	Gullet 2
X.661	*Synprioniodina bicurvata*	Sheinton 2
X.662	*Sagittodontus edentatus*	Gelli Farm 3
X.663	*Sagittodontus edentatus*	H.Q.3
X.664	*Sagittodontus edentatus*	West Malvern 1
X.665	*Exochognathus brassfieldensis*	H.V.4
X.666	*Exochognathus keislognathoides*	H.Q.3
X.667	*Exochognathus* sp. nov.	Plowden 2
X.668	*Exochognathus brevialatus*	New House, Marshbrook
X.669	*Exochognathus brevialatus*	Ticklerton 2
X.670	*Exochognathus latialatus*	Cowleigh Park 1
X.671	*Exochognathus latialatus*	Cowleigh Park 1
X.672	*Exochognathus detortus*	Sheinton 2
X.673	*Exochognathus detortus*	Cowleigh Park 1
X.674	*Exochognathus caudatus*	Cowleigh Park 1
X.675	*Plectospathodus extensus*	Cowleigh Park 1
X.676	*Plectospathodus extensus*	H.V.4
X.677	*Plectospathodus flexuosus*	Gullet 2
X.678	*Plectospathodus irregularis*	H.V.3
X.679	*Trichonodella? expansa*	Sheinton 2
X.680	*Trichonodella asymmetrica*	Sheinton 2
X.681	*Trichonodella symmetrica*	H.B.2
X.682	*Trichonodella symmetrica*	H.V.4
X.683	*Trichonodella symmetrica*	Gullet 2
X.684	*Trichonodella inconstans*	Sheinton 2
X.685	*Trichonodella excavata*	Ticklerton 3
X.686	*Lonchodina detorta*	H.V.4
X.687	*Lonchodina fluegeli*	H.V.4
X.688	*Lonchodina greilingi*	Gullet 2
X.689	*Lonchodina walliseri*	H.Q.3
X.690	*Lonchodina* sp. A	H.Q.1
X.691	*Lonchodina* sp. B	Plowden 2
X.692	*Lonchodina* sp. C	Ticklerton 3
X.693	gen. et sp. indet. A	Norbury 3
X.694	gen. et sp. indet. B	Sheinton 2
X.695	*Hindeodella equidentata*	Gullet 4
X.696	*Ligonodina kentuckyensis*	H.V.3
X.697	*Ligondina kentuckyensis*	Sheinton 2
X.698	*Ligonodina salopia*	Ticklerton 1
X.699	*Ligonodina silurica*	Sheinton 2
X.700	*Ligondina silurica*	Sheinton 2
X.701	*Ligonodina? variabilis*	Gullet 2
X.702	*Ligonodina petila*	Ticklerton 1
X 703	*Hibbardella? prima*	Plowden 3
X.704	*Hibbardella? trichonodelloides*	Gullet 4
X.705	*Hibbardella? trichonodelloides*	Cowleigh Park 1

Slide No.	*Conodont*	*Sample No.*
X.706	*Hibbardella* sp. nov.	Sheinton 2
X.707	*Hibbardella* sp. nov.	Sheinton 2
X.729	*Diadelognathus primus*	Norbury 1
X.708	*Acodus curvatus*	H.V.4
X.709	*Acodus unicostatus*	H.V.4
X.710	*Acodus unicostatus*	Gullet 2
X.711	*Distacodus obliquicostatus*	Minsterley Lane
X.712	*Drepanodus* sp.	Gelli Farm 3
X.713	*Drepanodus* sp.	Ticklerton Brook
X.714	*Drepanodus suberectus*	H.Q.3
X.715	*Drepanodus aduncus*	Cowleigh Park 1
X.716	*Panderodus unicostatus*	Sheinton 2
X.717	*Panderodus unicostatus*	Cowleigh Park 1
X.718	*Panderodus serratus*	H.Q.3
X.719	*Panderodus simplex*	H.Q.3
X.720	*Panderodus simplex*	Gullet 2
X.721	*Panderodus* cf. *P. staufferi*	H.B.1
X.722	*Panderodus* cf. *P. gracilis*	H.V.4
X.723	*Panderodus* cf. *P. gracilis*	Gullet 2
X.724	*Panderodus* sp. A	Cowleigh Park 1
X.725	*Paltodus debolti*	H.V.4
X.726	*Paltodus dyscritus*	H.V.4
X.727	*Paltodus migratus*	H.V.4
X.728	*Paltodus costulatus*	Cowleigh Park 1

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PLATE 1

All figures are ×35

Figs 1–3. ***Icriodella discreta*** Pollock, Rexroad & Nicoll

1. Oral view of specimen (X.585). 2. Oral view of specimen (X.586). 3. Outer lateral view of specimen (X.587).

Figs 4–7. ***Icriodella deflecta*** sp. nov.

4. Oral and aboral views of specimen S.1.4. 5. Oral view of specimen S.1.2. 6. Oral and outer lateral views of holotype (X.561). 7. Oral view of specimen (X.562).

Fig. 8. ***Icriodella*** cf. ***I. malvernensis*** sp. nov.

Oral view of specimen (X.571).

Figs 9–12. ***Icriodella malvernensis*** sp. nov.

9. Oral and outer views of specimen (X.569). 10. Aboral and oral views of holotype (X.567). 11. Oral view of specimen (X.570). 12. Oral view of specimen (X.568).

Figs 13–17. ***Icriodella inconstans*** sp. nov.

13. Oral view of specimen (X.564). 14. Oral view of specimen S.1.9. 15. Oral, aboral and outer lateral views of holotype (X.563). 16. Oral view of specimen (X.566). 17. Oral view of specimen (X.565).

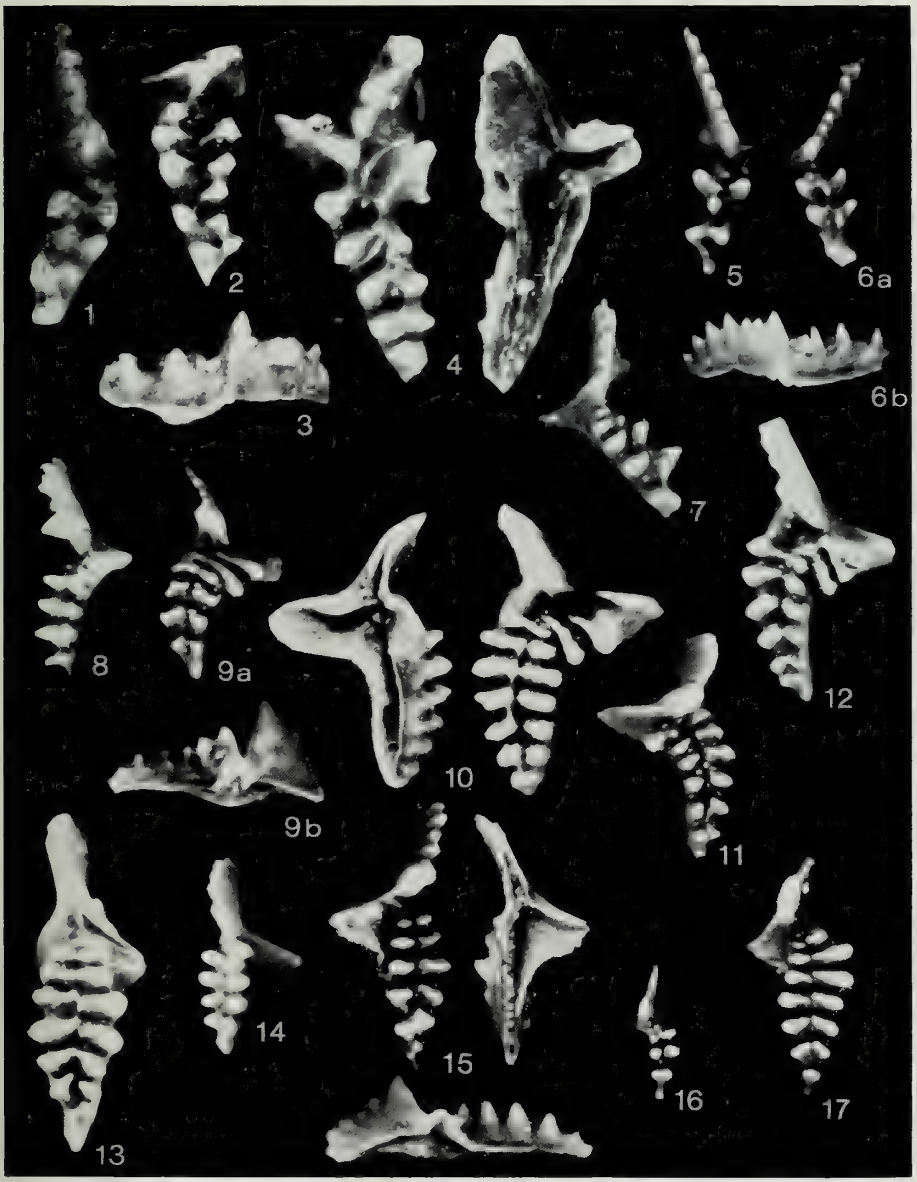
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PLATE 2

All figures are ×35

FIG. 1. ***Icriodina irregularis*** Branson & Branson

Aboral and oral views of specimen (X.588).

FIG. 2. ***Icriodina*** sp.

Aboral and oral views of specimen (X.589).

FIGS 3–4. ***Amorphognathus tenuis*** sp. nov.

3. Aboral and oral views of holotype (X.572). 4. Oral view of specimen (X.573).

FIG. 5. ***Astropentagnathus irregularis*** Mostler

Oral view of specimen (X.596).

FIG. 6. ***Aulacognathus kuehni*** Mostler

Oral view of specimen (X.595).

FIGS 7, 9. ***Apsidognathus tuberculatus*** Walliser

7. Aboral and oral views of specimen (X.593). 9. Oral view of specimen (X.594).

FIGS 8, 10, 11. ***Hadrognathus staurognathoides*** Walliser

8. Oral view of specimen (X.591). 10. Oral and aboral views of specimen (X.592).
11. Oral view of specimen (X.590).

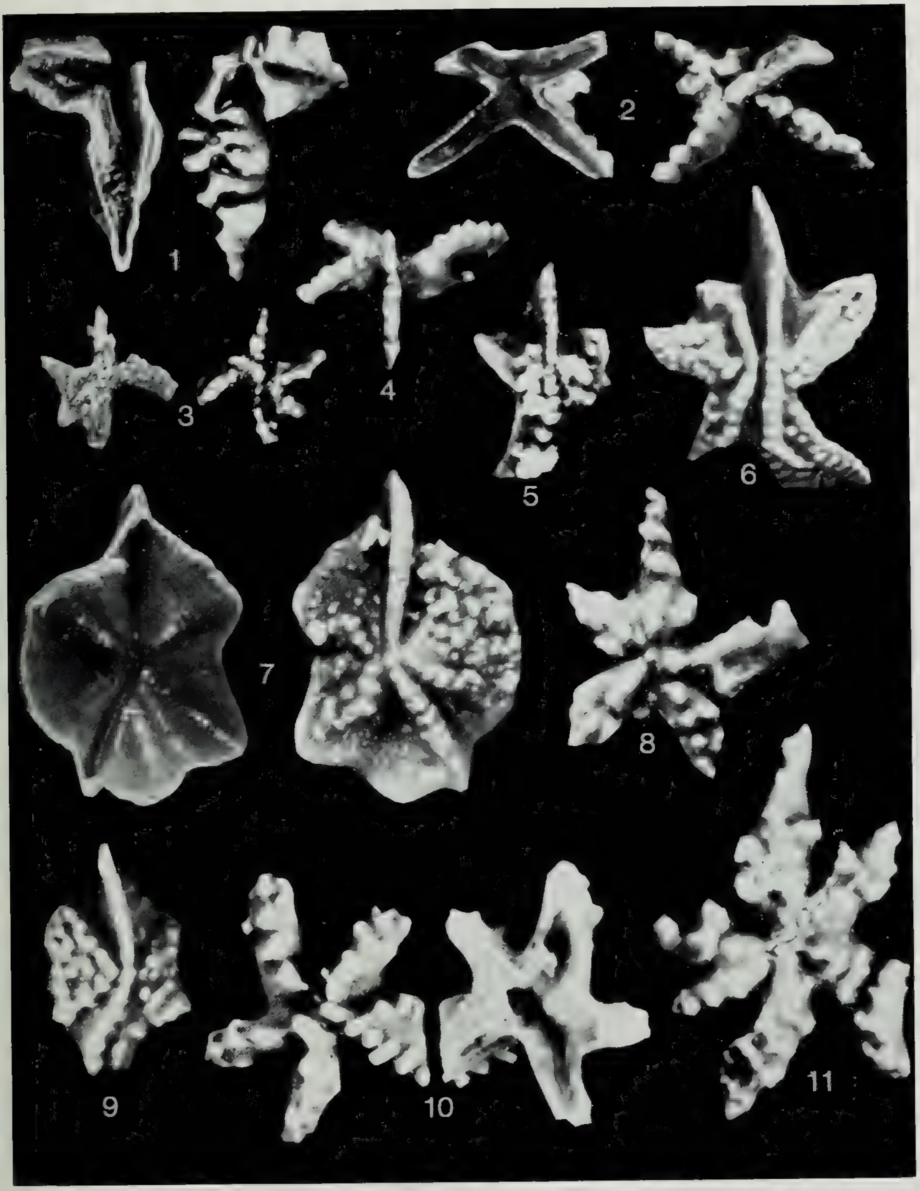
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PLATE 3

All figures are ×35

FIG. 1. ***Astrognathus tetractis*** Walliser

Oral and aboral views of specimen (X.608).

FIG. 2. ***Pygodus? lyra*** Walliser

Oral and aboral views of specimen (X.609).

FIG. 3. ***Aphelognathus siluricus*** Pollock, Rexroad & Nicoll

Lateral and oral views of specimen (X.618).

FIG. 4. ***Ambalodus anapetus*** Pollock, Rexroad & Nicoll

Lateral and oral views of specimen (X.619).

FIG. 5. ***Ambalodus*** sp.

Lateral and oral views of specimen (X.620).

FIGS 6, 8. ***Ambalodus galerus*** Walliser

6. Lateral view of specimen (X.622). 8. Lateral and oral views of specimen (X.623).

FIG. 7. ***Ambalodus triangularis*** Branson & Mehl

Lateral and oral views of specimen (X.621).

FIGS 9–12. ***Neospathognathodus celloni*** (Walliser)

9. Lateral view of specimen (X.597). 10. Lateral view of specimen (X.598). 11. Lateral view of specimen (X.599). 12. Oral view of specimen (X.600).

FIGS 13, 16. ***Neospathognathodus pennatus*** (Walliser)

13. Oral and lateral views of specimen (X.601). 16. Oral view of specimen (X.602).

FIG. 14. ***Neospathognathodus?*** sp.

Oral and lateral views of specimen (X.603).

FIG. 15. ***Neospathognathodus bullatus*** Nicoll & Rexroad

Oral view of specimen (X.604).

FIGS 17–19. ***Pterospathodus amorphognathoides*** Walliser

17. Oral view of specimen (X.606). 18. Oral view of specimen (X.607). 19. Oral, lateral and aboral views of specimen (X.605).

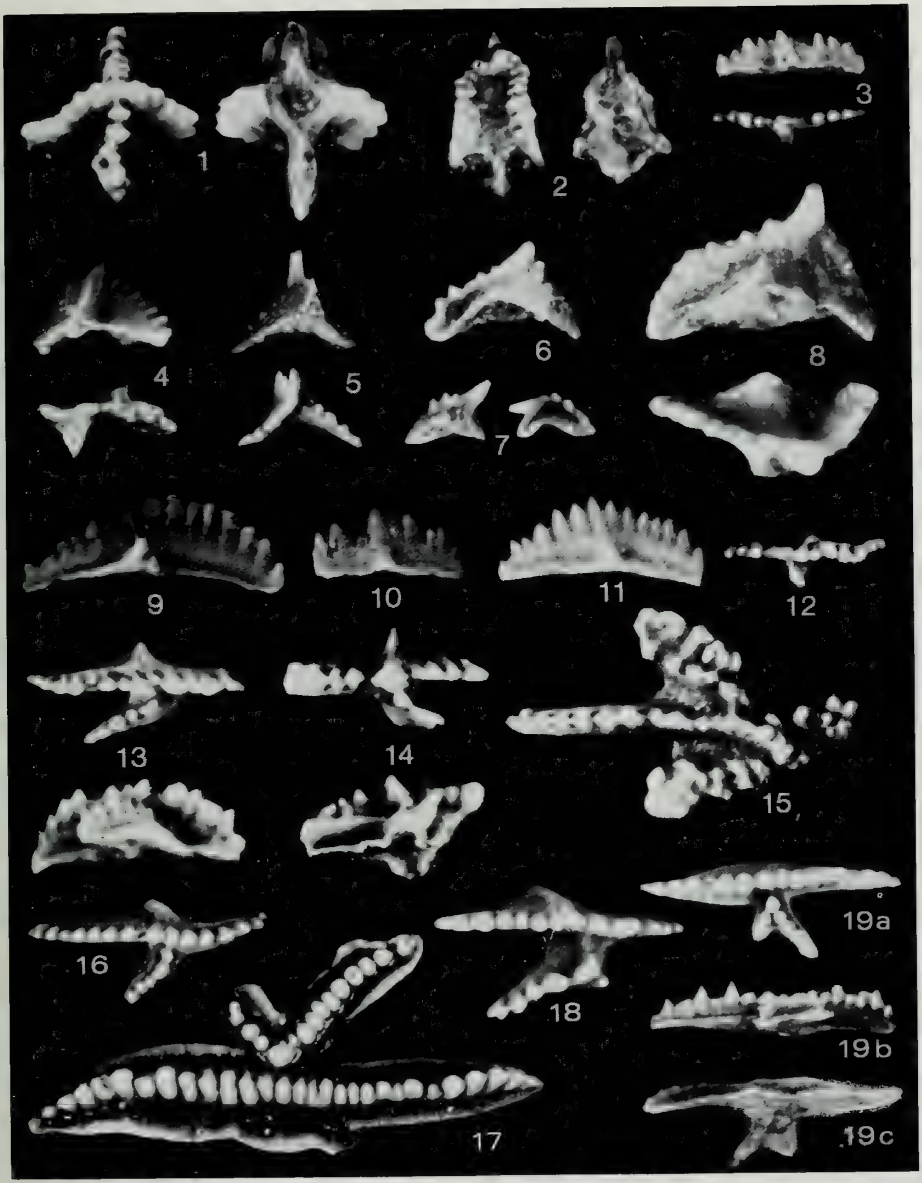
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PLATE 4

All figures are ×35

FIG. 1. ***Spathognathodus oldhamensis*** Rexroad

Lateral and oral views of specimen (X.626).

FIGS 2, 3. ***Spathognathodus hassi*** Pollock, Rexroad & Nicoll

2. Lateral and oral views of specimen (X.624). 3. Lateral and oral views of specimen (X.625).

FIG. 4. ***Spathognathodus*** sp. nov. A

Lateral and oral views of specimen S.3.9.

FIG. 5. ***Spathognathus*** sp. nov. B

Lateral and oral views of specimen (X.629).

FIGS 6, 7. ***Spathognathodus abruptus*** sp. nov.

6. Outer lateral and oral views of holotype (X.574). 7. Outer lateral and oral views of specimen (X.575).

FIG. 8. ***Spathognathodus*** cf. ***S. abruptus*** sp. nov.

Oral view of specimen (X.576).

FIGS 9–12. ***Spathognathodus gulletensis*** sp. nov.

9. Lateral and oral views of holotype (X.577). 10. Lateral view of specimen (X.578). 11. Oral view of specimen S.1.37. 12. Lateral view of specimen (X.580).

FIG. 13. ***Spathognathodus polinclinatus*** Nicoll & Rexroad

Lateral view of specimen S.3.8.

FIG. 14. ***Spathognathodus ranuliformis*** Walliser

Lateral and oral views of specimen (X.630).

FIGS 15, 16. ***Spathognathodus inclinatus*** (Rhodes)

15. Lateral view of specimen (X.628). 16. Lateral view of specimen (X.627).

FIG. 17. ***Ozarkodina*** cf. ***O. edithae*** Walliser

Lateral view of specimen (X.632).

FIGS 18–20. ***Ozarkodina typica*** Branson & Mehl

18. Lateral view of specimen (X.637). 19. Lateral view of specimen (X.638). 20. Lateral view of specimen (X.639).

FIG. 21. ***Ozarkodina media*** Walliser

Lateral view of specimen (X.636).

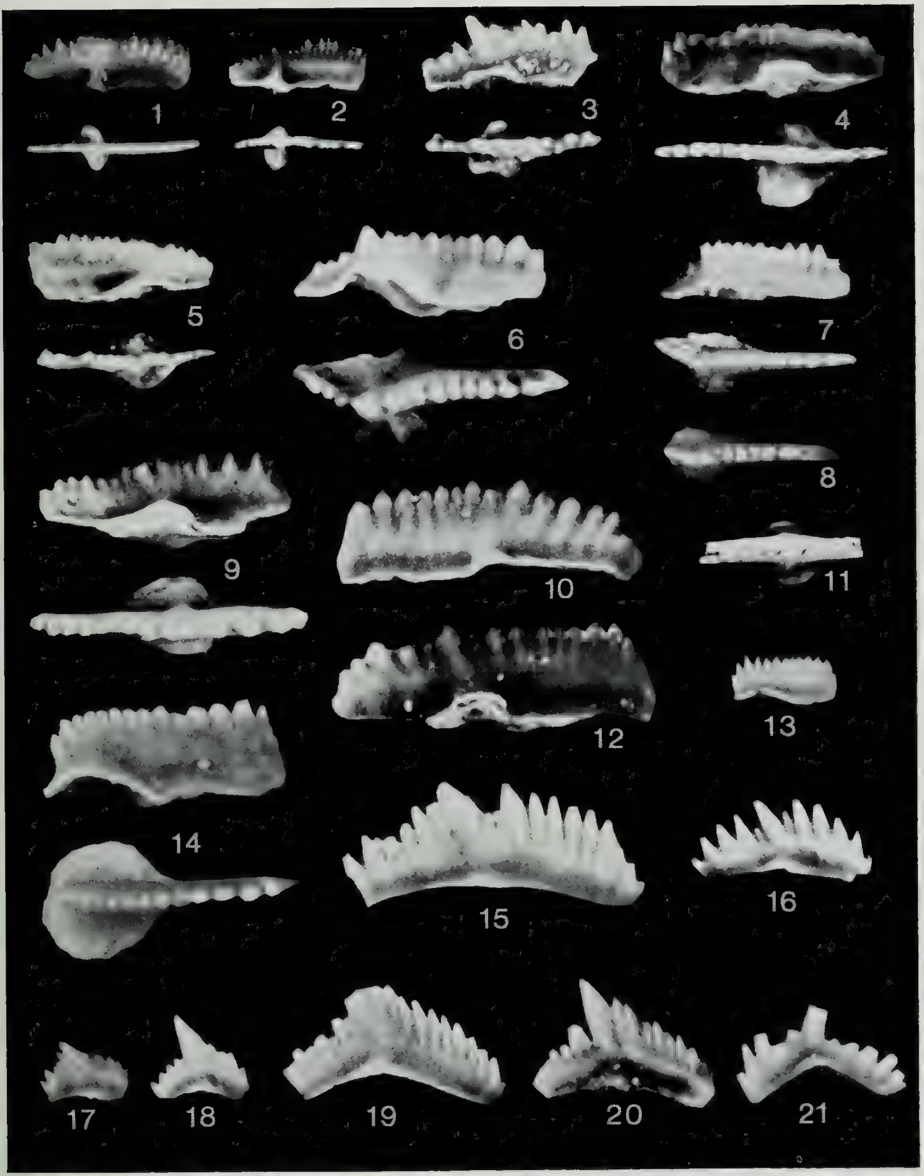
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PLATE 5

All figures are ×35

FIG. 1. ***Ozarkodina hanoverensis*** Nicoll & Rexroad

Lateral view of specimen (X.635).

FIGS 2, 3. ***Ozarkodina adiutricis*** Walliser

2. Lateral view of specimen S.3.12. 3. Lateral view of specimen (X.631).

FIGS 4, 6. ***Ozarkodina alisonae*** sp. nov.

4. Lateral views of holotype (X.581). 6. Lateral view of specimen (X.582).

FIGS 5, 7. ***Ozarkodina gaertneri*** Walliser

5. Lateral views of specimen (X.634). 7. Lateral view of specimen (X.633).

FIGS 8–10. ***Carniodus carinthiacus*** Walliser

8. Lateral view of specimen S.2.64. 9. Lateral view of specimen S.2.65. 10. Lateral view of specimen (X.610).

FIG. 11. ***Carniodus carnicus*** Walliser

Lateral view of specimen (X.611).

FIGS 12–14. ***Carniodus carnulus*** Walliser

12. Lateral view of specimen (X.612). 13. Lateral view of specimen (X.613). 14. Lateral view of aberrant specimen (X.614).

FIGS 15, 16. ***Carniodus carnus*** Walliser

15. Lateral view of specimen (X.615). 16. Lateral view of specimen S.2.72.

FIG. 17. ***Neoprioniodus subcarnus*** Walliser

Lateral view of specimen (X.659).

FIG. 18. ***Carniodus*** cf. ***C. carnus*** Walliser

Lateral view of specimen (X.616).

FIG. 19. ***Carniodus*** cf. ***C. eocarnicus*** Walliser

Lateral view of specimen (X.617).

FIGS 20, 21. ***Neoprioniodus costatus paucidentatus*** Walliser

20. Inner lateral view of specimen (X.652). 21. Inner lateral view of specimen (X.653).

FIGS 22. ***Neoprioniodus costatus costatus*** Walliser

Inner lateral view of specimen (X.654).

FIG. 23. ***Neoprioniodus planus*** Walliser

Inner lateral view of specimen (X.658).

FIG. 24. ***Neoprioniodus latidentatus*** Walliser

Inner lateral view of specimen (X.656).

FIG. 25. ***Neoprioniodus excavatus*** (Branson & Mehl)

Inner lateral view of specimen (X.655).

FIG. 26. ***Neoprioniodus multiformis*** Walliser

Inner lateral view of specimen (X.657).

FIG. 27. ***Synprioniodina silurica*** Walliser

Inner lateral view of specimen (X.660).

FIG. 28. ***Synprioniodina bicurvata*** (Branson & Mehl)

Inner lateral view of specimen (X.661).

FIG. 29. gen. et sp. indet. B

Oral and lateral views of specimen (X.694).

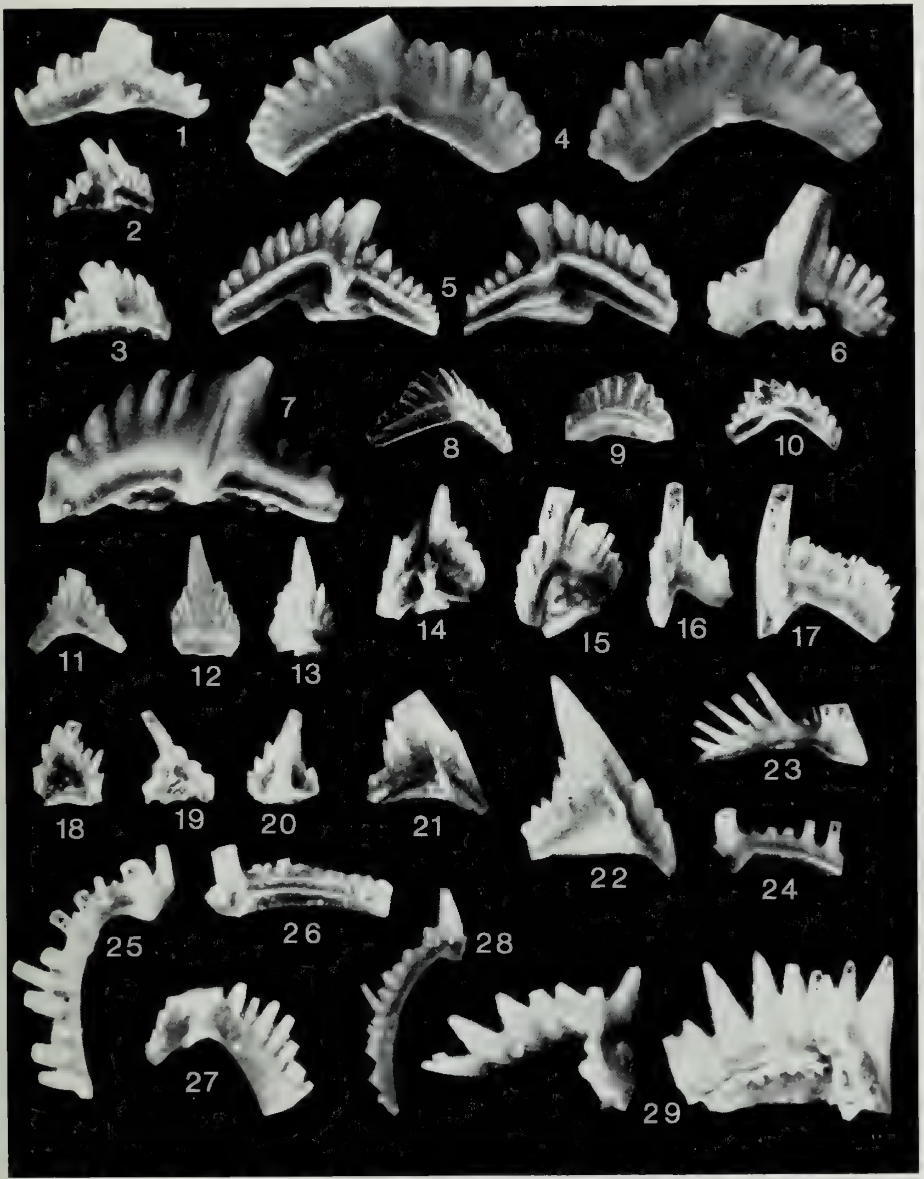
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PLATE 6

All figures are ×35

FIG. 1. ***Gothodus?*** sp. nov.

Lateral views of specimen (X.649).

FIG. 2. ***Distomodus? extrorsus*** (Rexroad)

Inner lateral and outer lateral views of specimen (X.640)

FIGS 3, 4, 9. ***Distomodus? egregius*** (Walliser)

3. Outer lateral view of specimen (X.641). 4. Outer lateral and inner lateral views of specimen (X.643). 9. Outer lateral and inner lateral views of specimen (X.642).

FIGS 5–8, 11. ***Distomodus kentuckyensis*** Branson & Branson

5. Inner lateral view of specimen (X.645). 6. Inner lateral view of specimen (X.646). 7. Inner lateral view of specimen (X.647). 8. Inner lateral view of specimen (X.644). 11. Inner lateral view of specimen (X.648).

FIG. 10. ***Distomodus*** sp. nov.

Inner lateral and outer lateral views of specimen S.3.30.

FIG. 12. ***Distomodus triangularis triangularis*** (Walliser)

Inner lateral view of specimen (X.651).

FIG. 13. ***Distomodus triangularis tenuirameus*** (Walliser)

Inner lateral view of specimen (X.650).

FIGS 14, 15. ***Hibbardella*** sp. nov.

14. Oral and lateral views of specimens (X.706). 15. Posterior view of specimen (X.707).

FIG. 16. ***Hibbardella? prima*** (Walliser)

Posterior view of specimen (X.703).

FIGS 17, 18. ***Hibbardella? trichonodelloides*** (Walliser)

17. Aboral and oral views of specimen (X.704). 18. Lateral view of specimen (X.705).

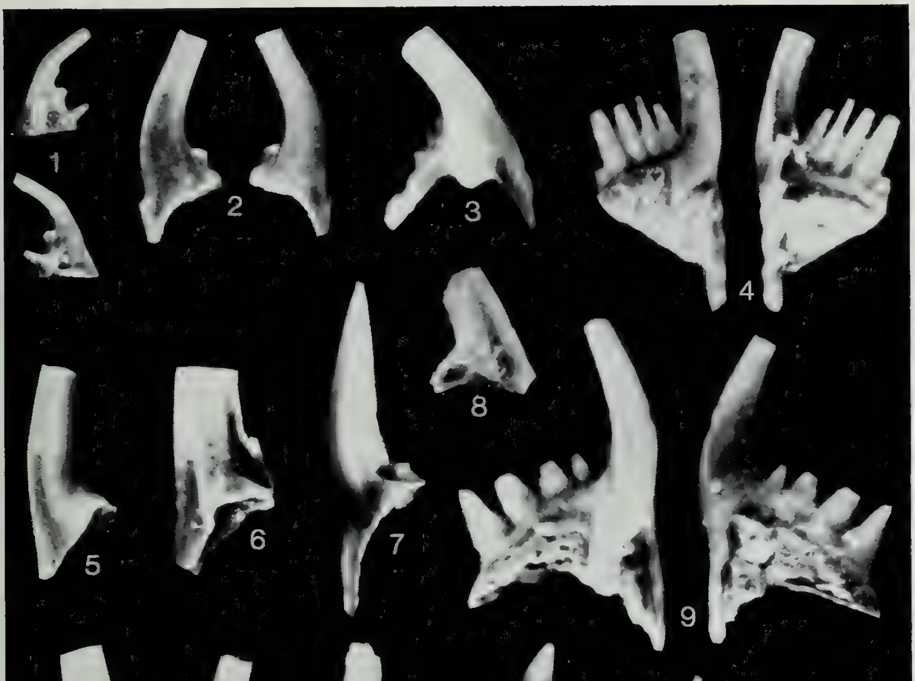
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PLATE 7

All figures are ×35

FIGS 1–3. ***Sagittodontus edentatus*** (Branson & Branson)

1. Posterior and inner lateral views of specimen (X.662). 2. Posterior view of specimen (X.663). 3. Posterior view of specimen (X.664).

FIG. 4. ***Exochognathus brassfieldensis*** (Branson & Branson)

Posterior view of specimen (X.665).

FIG. 5. ***Exochognathus keislognathoides*** Pollock, Rexroad & Nicoll

Posterior view of specimen (X.666).

FIG. 6. ***Exochognathus*** sp. nov.

Posterior view of specimen (X.667).

FIGS 7, 12. ***Exochognathus detortus*** (Walliser)

7. Lateral and posterior views of specimen (X.673). 12. Posterior and lateral views of specimen (X.672).

FIGS 8, 9. ***Exochognathus brevialatus*** (Walliser)

8. Posterior view of specimen (X.669). 9. Posterior view of specimen (X.668).

FIGS 10, 11. ***Exochognathus latialatus*** (Walliser)

10. Posterior view of specimen (X.670). 11. Lateral view of specimen (X.671).

FIG. 13. ***Exochognathus caudatus*** (Walliser)

Lateral view of specimen (X.674).

FIG. 14. ***Trichonodella? expansa*** Nicoll & Rexroad

Lateral, oral and posterior views of specimen (X.679).

FIGS 15, 18, 19. ***Trichonodella symmetrica*** (Branson & Mehl)

15. Posterior view of specimen (X.681). 18. Posterior view of specimen (X.682). 19. Posterior view of specimen (X.683).

FIG. 16. ***Trichonodella inconstans*** Walliser

Posterior view of specimen (X.684).

FIG. 17. ***Trichonodella asymmetrica*** Nicoll & Rexroad

Posterior view of specimen (X.680).

FIG. 20. ***Trichonodella excavata*** (Branson & Mehl)

Posterior view of specimen (X.685).

FIGS 21, 22. ***Plectospathodus extensus*** Rhodes

21. Posterior view of specimen (X.675). 22. Posterior view of specimen (X.676).

FIG. 23. ***Plectospathodus irregularis*** (Branson & Branson)

Posterior view of specimen (X.678).

FIG. 24. ***Plectospathodus flexuosus*** Branson & Mehl

Posterior view of specimen (X.677).

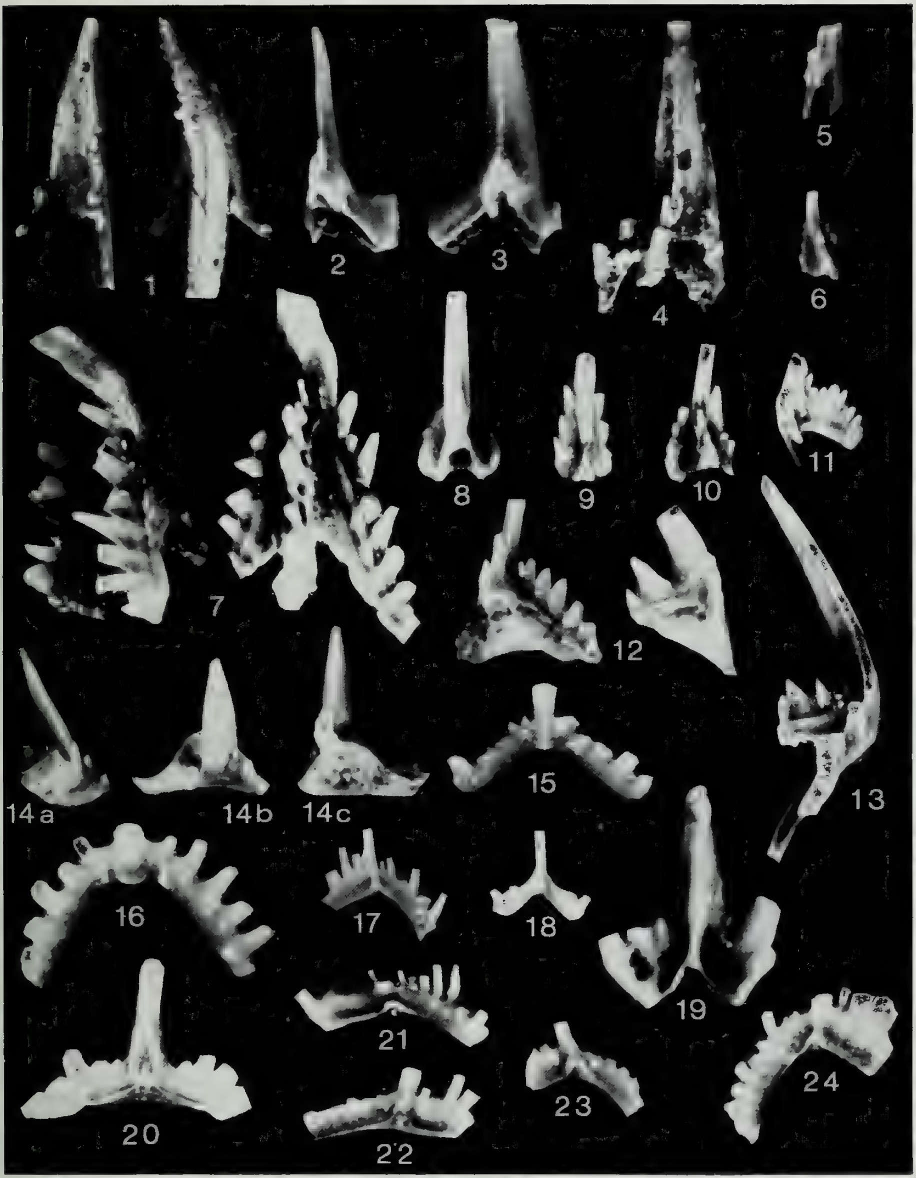
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PLATE 8

All figures are ×35

FIG. 1. ***Diadelognathus primus*** Nicoll & Rexroad

Oral and aboral views of specimen (X.729).

FIGS 2, 3. ***Diadelognathus nicolli*** sp. nov.

2. Lateral view of specimen (X.584). 3. Aboral and oral views of holotype (X.583).

FIG. 4. ***Lonchodina greilingi*** Walliser

Lateral view of specimen (X.688).

FIG. 5. ***Lonchodina walliseri*** Ziegler

Lateral view of specimen (X.689).

FIG. 6. ***Lonchodina detorta*** Walliser

Oral and lateral views of specimen (X.686).

FIG. 7. ***Lonchodina fluegeli*** Walliser

Oral and aboral views of specimen (X.687).

FIG. 8. ***Lonchodina*** sp B

Lateral view of specimen (X.691).

FIG. 9. ***Lonchodina*** sp. A

Aboral view of specimen (X.690).

FIGS 10, 13. ***Ligonodina silurica*** Branson & Mehl

10. Inner lateral view of specimen (X.699). 13. Inner lateral view of specimen (X.700).

FIG. 11. ***Ligonodina petila*** Nicoll & Rexroad

Inner lateral view of specimen (X.702).

FIG. 12. ***Lonchodina*** sp. C

Lateral view of specimen (X.692).

FIG. 14. ***Ligonodina? variabilis*** Nicoll & Rexroad

Inner lateral view of specimen (X 701)

FIGS 15, 16. ***Ligonodina kentuckyensis*** Branson & Branson

15 Inner lateral view of specimen (X.696). 16. Inner lateral view of specimen (X.697).

FIG. 17. ***Ligonodina salopia*** Rhodes

Inner lateral view of specimen (X.698).

FIG. 18. gen. et sp. indet. A

Lateral view of specimen (X.693).

FIG. 19. ***Hindeodella equidentata*** Rhodes

Inner lateral view of specimen (X.695).

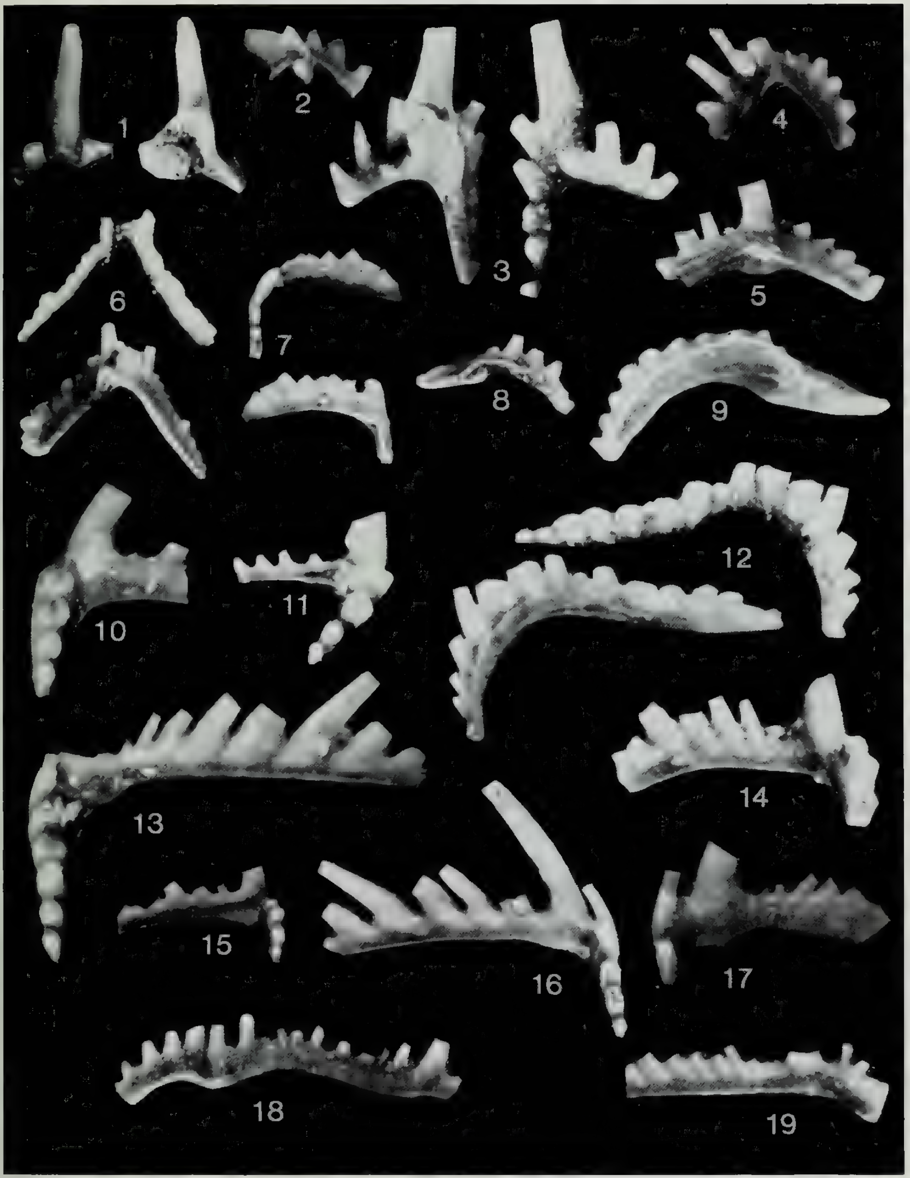
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PLATE 9

All figures are ×35

FIG. 1. ***Acodus curvatus*** Branson & Branson

Inner lateral and outer lateral views of specimen (X.708).

FIGS 2, 3. ***Acodus unicostatus*** Branson & Branson

2. Inner lateral and outer lateral views of specimen (X.709). 3. Outer lateral view of specimen (X.710).

FIG. 4. ***Distacodus obliquicostatus*** Branson & Mehl

Lateral views of specimen (X.711).

FIGS 5, 6. ***Panderodus unicostatus*** (Branson & Mehl)

5. Lateral view of specimen (X.716). 6. Lateral views of specimen (X.717).

FIG. 7. ***Panderodus serratus*** Rexroad

Lateral view of specimen (X.718).

FIGS 8, 9. ***Panderodus simplex*** (Branson & Mehl)

8. Lateral views of specimen (X.719). 9. Lateral view of specimen (X.720).

FIG. 10. ***Panderodus*** cf. ***P. staufferi*** (Branson, Mehl & Branson)

Lateral views of specimen (X.721).

FIG. 11. ***Panderodus*** sp. A

Lateral views of specimen (X.724).

FIGS 12, 13. ***Panderodus*** cf. ***P. gracilis*** (Branson & Mehl)

12. Lateral views of specimen (X.722). 13. Lateral view of specimen (X.723).

FIG. 14. ***Drepanodus*** sp.

Lateral view of specimen (X.712).

FIG. 15. ***Drepanodus*** sp.

Lateral view of specimen (X.713).

FIG. 16. ***Drepanodus suberectus*** (Branson & Mehl)

Lateral view of specimen (X.714).

FIG. 17. ***Drepanodus aduncus*** Nicoll & Rexroad

Lateral view of specimen (X.715).

FIG. 18. ***Paltodus debolti*** Rexroad

Outer lateral and inner lateral views of specimen (X.725).

FIG. 19. ***Paltodus dyscritus*** Rexroad

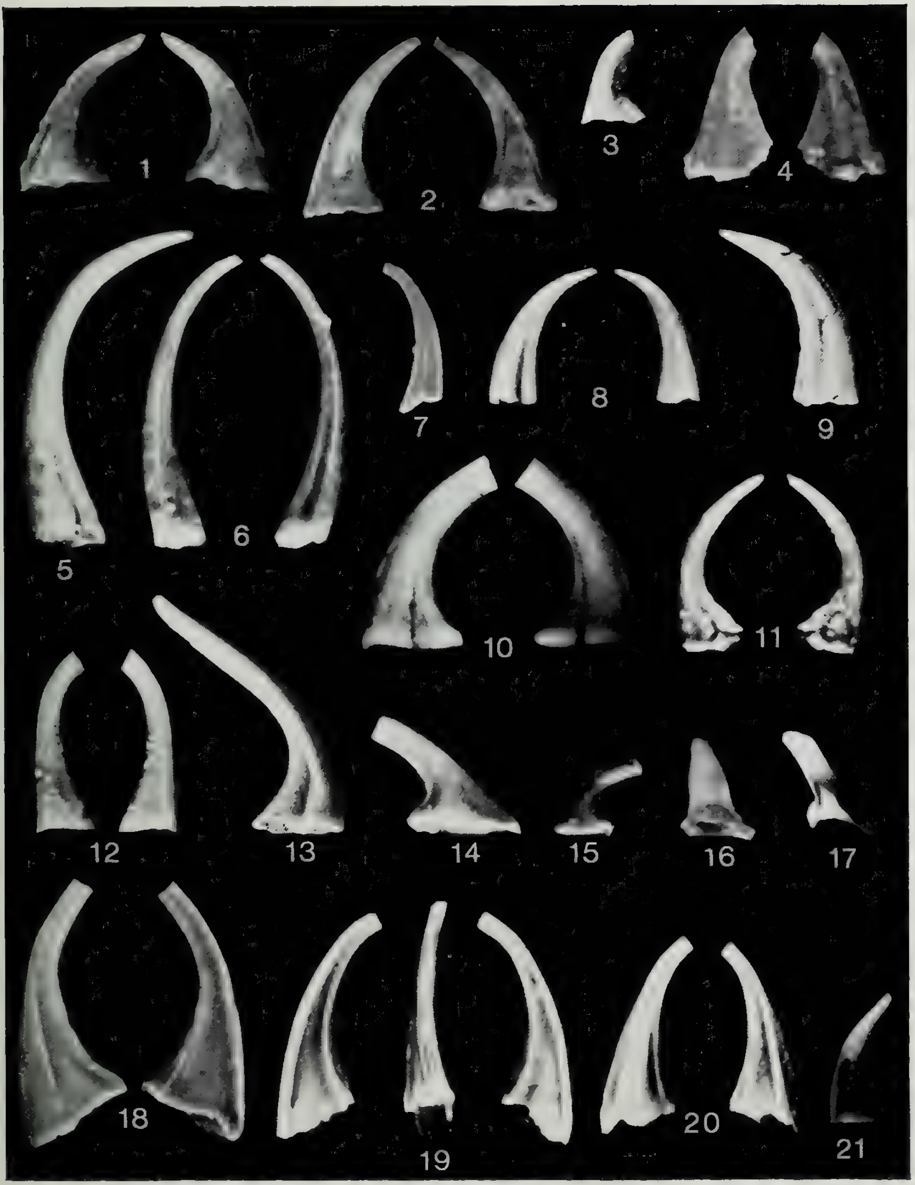
Lateral, posterior and lateral views of specimen (X.726).

FIG. 20. ***Paltodus migratus*** Rexroad

Lateral views of specimen (X.727).

FIG. 21. ***Paltodus costulatus*** Rexroad

Lateral view of specimen (X.728).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A REVISION OF THE REDFIELDIIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKER'S KRAAL (SOUTH AFRICA) AND BROOKVALE (NEW SOUTH WALES)

P. HUTCHINSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 3
LONDON : 1973

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NATURAL HISTORY

A REVISION OF THE REDFIELDIIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKER'S KRAAL (SOUTH AFRICA) AND BROOKVALE (NEW SOUTH WALES)

BY

PETER HUTCHINSON
Drayton, Berks., England

Pp. 233-354; 54 *Text-figures*

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A REVISION OF THE REDFIELDIIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKER'S KRAAL (SOUTH AFRICA) AND BROOKVALE (NEW SOUTH WALES)

By PETER HUTCHINSON

CONTENTS

Page

I. INTRODUCTION 236

II. SYSTEMATIC DESCRIPTIONS 238

- Order REDFIELDIIFORMES 238
  - Family Brookvaliidae 239
    - Genus *Ischnolepis* Haughton 239
      - *I. bancrofti* Haughton 240
    - Genus *Atopocephala* Brough 249
      - *A. watsoni* Brough 250
    - Genus *Brookvalia* Wade 251
      - *B. gracilis* Wade 252
      - *B. parvisquamata* Wade 259
      - *B. propennis* Wade 259
      - *B. latipennis* (Wade) comb. nov. 262
      - *B. spinosa* (Wade) comb. nov. 264
    - Genus *Phlyctaenichthys* Wade 267
      - *P. pectinatus* Wade 269
  - Family Redfieldiidae 271
    - Genus *Daedalichthys* Brough 271
      - *D. higginsi* Brough 273
    - Genus *Helichthys* Broom 274
      - *H. elegans* Brough 275
    - Genus *Geitonichthys* Wade 277
      - *G. ornatus* Wade 277
    - Genus *Molybdichthys* Wade 280
      - *M. junior* Wade 281
  - Family Schizurichthyidae nov. 285
    - Genus *Schizurichthys* Wade 285
      - *S. pulcher* Wade 285
  - Genera provisionally ascribed to Redfieldiiformes . . . 289
- Order PERLEIDIFORMES 292
  - Family Colobodontidae 292
    - Genus *Meidiichthys* Brough 292
      - *M. browni* (Broom) 293
    - Genus *Procheirichthys* Wade 295
      - *P. ferox* Wade 295

Genus *Manlietta* Wade 297
M. crassa Wade 298
Family Cleithrolepididae 302
Genus *Cleithrolepidina* Berg. 302
C. minor (Broom) 303
C. extoni (Woodward) comb. nov. 305
Genus *Cleithrolepis* Egerton 311
C. granulata Egerton 212
Family Hydropessidae nov. 316
Genus *Hydropessum* Broom. 316
H. kannemeyeria Broom 316
Genera provisionally ascribed to Perleidiformes . . 321
III. Discussion 321
(a) Classification of the Redfieldiiformes. 321
(i) Brookvaliidae and Redfieldiidae 321
(ii) Schizurichthyidae 323
(iii) Redfieldiiformes–discussion 324
(b) A functional analysis of the redfieldiiform skull . . . 325
(i) Gill ventilation 326
(ii) Feeding 326
(c) Growth of the tail in *Brookvalia*, and some notes on palaeoniscoid body lobe squamation 328
(d) Classification of the Perleidiformes 333
(i) Colobodontidae 333
(ii) Cleithrolepididae and Hydropessidae . . . 335
(e) Evolution of the Perleidiformes 338
(i) Cleithrolepididae 338
(ii) Hydropessidae 342
(f) Origin of Redfieldiiformes and Perleidiformes . . . 343
IV. Summary 347
V. Acknowledgements 349
VI. Abbreviations 349
VII. References 350

SYNOPSIS

All the genera included in the Redfieldiiformes and Perleidiformes (Chondrostei) from the Triassic localities at Bekker's Kraal (South Africa) and Brookvale (New South Wales) are redescribed. In addition, *Ischnolepis*, an early redfieldiiform from Zambia is redescribed. The order Redfieldiiformes is divided into three families; the Brookvaliidae, the Redfieldiidae and the Schizurichthyidae nov. The order Perleidiformes is divided into four families; the Aetheodontidae, the Colobodontidae, the Cleithrolepididae and the Hydropessidae, a new family erected for the inclusion of *Hydropessum*, a genus previously thought to be a cleithrolepid. A functional analysis is made of the redfieldiiform skull and it is concluded that the Redfieldiidae possessed a unique suctorial feeding mechanism. Growth and development of the tail in *Brookvalia gracilis* is described, and the palaeoniscoid body lobe squamation is discussed. It is concluded that reversal of body lobe scale rows does not occur in palaeoniscoids.

I. INTRODUCTION

TRIASSIC fish from Bekker's Kraal were first described by Broom (1909) and subsequently by Brough (1931, 1934) while those from Brookvale, N.S.W. were described by Wade (1935). It is clear from more recent publications on Triassic fish that comparative studies have been limited by the incomplete nature of these earlier descriptions (see, for example, Schaeffer 1955 : text-figs 7 and 8; 1967 : text-figs 17 and 18), and a redescription of the Redfieldiiformes and Perleidiformes from Brookvale and Bekker's Kraal has been attempted to remedy this. In addition it was clear that a redescription of *Ischnolepis* from Zambia (Haughton 1934) would help in an attempt to understand the early redfieldiids.

With the exception of *Ischnolepis*, the specimens described here required no preparation. The Brookvale specimens are impressions and natural casts of fish which have been crushed to a thickness of at most a few millimetres. The Bekker's Kraal fossils are, in the main, impressions, although replacement minerals are sometimes present.

Of the material studied here, only *Ischnolepis* was preserved in a relatively uncrushed state. Specimens of this genus were preserved in a matrix of acid resistant, fine grained mudstone, and I have been able to remove this matrix with an ultrasonic probe, revealing many new features. The ages of the three localities will now be discussed briefly:

Zambia. The locality of the type material of *Ischnolepis bancrofti* is the Lunsempfwa valley, Zambia (lower part), and is described as 'probably Upper Beaufort or Lower Stormberg' (Haughton 1934 : 97). However, specimens of *I. bancrofti* in the British Museum (Natural History) are registered as coming from the Madumabisa shales, 82 miles from Kabwe (Broken Hill), and north of the junction between Tutenge and Lunsempfwa rivers, at latitude 14°43′ south, and longitude 29°38′ east. The Madumabisa mudstones and shales are generally thought to extend from Ecca formation times to the Cistecephalus zone, therefore not extending beyond the uppermost Permian (Gair, 1960 : 9; Drysdall & Kitching, 1963 : 34). It has been suggested, however, that plant remains from the uppermost parts of the Madumabisa mudstone in Rhodesia indicate that these beds in fact extend to the top of the Beaufort Series, and that they include a condensed succession which is equivalent to the Lystrosaurus and Cynognathus zones (Bond 1965). This extension of the possible upper limits of the Madumabisa mudstones to include the Lower Triassic epoch means that, unless the locality of *I. bancrofti* is more exactly identified, its probable age can only be defined as uppermost Permian or Scythian.

Bekker's Kraal. The Bekker's Kraal fish are found in a sandstone layer 20 mm thick which occurs in a 10 metre thick bed of sandstone which, in turn, forms part of the lower Cynognathus zone succession in Orange Free State (Watson 1931). They are therefore Scythian in age—Upper Scythian according to Romer (1947) or Lower Scythian according to Cosgriff (1969).

Gosford, Brookvale and St. Peters. These three Australian localities occur in the Sydney basin where the Triassic is divided into three groups: Narrabeen, Hawkesbury and Wianamatta. These are subdivided as follows (youngest at top):

WIANAMATTA	Camden Subgroup	
	Liverpool Subgroup (including the Ashfield shale)	ST. PETERS FAUNA
HAWKESBURY	Hawkesbury sandstone	BROOKVALE FAUNA

NARRABEEN	Gosford formation Collaroy claystone Tuggerah formation Munmorah conglomerate	GOSFORD FAUNA

(Banks *et al.* 1969)

The Munmorah conglomerate overlies the Newcastle Coal Measures, the uppermost coal seam of which traditionally marks the upper limit of the Permian. However, the validity of this boundary has been questioned by several authors because various coal seams appear to have been regarded as being the uppermost in various localities. The Permo-Triassic contact may in fact be 'an undulating surface with marked relief' (Balme 1969 : 108). Moreover, the lower part of the Munmorah conglomerate contains a Permian flora including *Glossopteris*, *Schizoneura*, *Phyllotheca* and *Cladophlebis*, while the upper part contains the first record of the spore *Aratrisporites*, which is characteristic of Lower Triassic strata in many parts of the world (Helby 1966). The true Permo-Triassic contact probably therefore lies within the Munmorah conglomerate.

Above the Munmorah conglomerate there are about 2000 feet of shales and sandstone (Wade 1941b) which, if the age of the Permo-Triassic boundary given above is correct, may be regarded as representing the Scythian. Obviously, with no further information, it is not possible to say whether these sediments represent part or all of the Scythian, or even whether they extend into the Anisian. The Gosford fish fauna, which is found in the uppermost of these beds, is therefore very tentatively placed at the Scythian/Anisian boundary.

There are 550 feet of sandstones (the lower part of the Hawkesbury sandstone) between the Gosford and Brookvale horizons (Wade 1935), but within these sediments there are signs of an erosional hiatus, and incomplete palynological data indicate that this may represent a substantial time break (Helby, pers. comm). The Brookvale fauna may therefore be considerably younger than that of Gosford, and is here tentatively regarded as being Ladinian in age.

II. SYSTEMATIC DESCRIPTIONS

Order REDFIELDIIFORMES

DIAGNOSIS. Small to moderately large fusiform chondrostean fishes. Skull bones usually ornamented with ridges or tubercles. Skull roof composed of extrascapulars, parietals, dermosphenotic, frontals and dermopterotic. Extrascapulars and parietals sometimes divided. Dermopterotic deep, dermosphenotic either rectangular or crescent-shaped. A postrostral may or may not be present. Snout composed of nasals, antorbitals and rostral, and sometimes adnasals and premaxillae. A single nostril present. Nasals small, bordering dorsal edge of nostril. Antorbital bordering anterior edge of orbit and ventral edge of nostril and, in forms which lack premaxillae, the ventral edge of the snout. Opercular series oblique to vertical, composed of opercular, subopercular and one, or rarely two, plate-like branchiostegals. Preopercular high and 'r'-shaped. Maxilla expanded posteriorly and attached to cheek. Teeth conical and pointed. Braincase of palaeoniscoid type.

Scales rhombic to leaf-shaped or, in the Schizurichthyidae, rectangular to subcircular with peg and socket articulation; dentine layer absent. Dorsal and anal fin-rays more numerous than endoskeletal supports, jointed and bifurcated; leading rays usually bearing fringing fulcra. Jointing and fringing fulcra often reduced in paired fin-rays. Caudal fin with abbreviated body lobe.

Family **BROOKVALIIDAE** Berg 1940

Diagnosis. Orbit large. Two pairs of parietals (except in *Atopocephala*). Dermopterotic deeper than dermosphenotic. Posterior extension of supraorbital sensory canal, if present, on dermopterotic. Dermosphenotic narrow and crescent-shaped, tapering to a point anteriorly. Frontal curved, and running close to, or actually touching, orbital edge. Snout composed of rostral, and paired antorbitals, nasals and premaxillae. Postrostral present in some genera, probably lost in *Atopocephala*. Antorbital a narrow curved element, bordering the anterior edge of the orbit, with a narrow anterior extension bordering the ventral edge of the nostril. Antorbital separated from the ventral edge of snout by premaxilla. Adnasal absent, or, if present, small and diamond-shaped, having no contact or point contact with dermosphenotic. A single dermohyal present. An antopercular present. Infraorbital elements either separating maxilla from orbital edge or reduced so that maxilla actually borders orbital edge for a short distance. Gular plate present. Lower jaw slender, long and curved dorsally towards the symphysis. Elements of pectoral girdle generally narrow. Fulcra on dorsal and anal fins small or absent. Scales rhomboidal to leaf-shaped. Hinge line at base of body lobe not usually marked by abrupt change in orientation of scales.

Genus ***ISCHNOLEPIS*** Haughton 1934

1934 *Ischnolepis* Haughton: 97.

Diagnosis (emended). Head bullet-shaped with an extremely large orbit anteriorly placed. Skull bones ornamented with small tubercles. Two pairs of parietals, posterior element triangular, though smaller than in *Brookvalia*. Dermopterotic rectangular. No extension of the supraorbital sensory canal on dermopterotic. Frontal extending anteriorly just beyond the level of the midpoint of the orbit. Opercular series longer than in *Brookvalia*, and moderately oblique. Preopercular with an antero-ventral extension running for a short distance above the antero-dorsal edge of the maxilla. Infraorbital elements very narrow. Teeth slightly recurved.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped, each ornamented with a row of tubercles. Jointing regular on all fin-rays except on those of the pectoral fin. Anal fin opposite the dorsal fin, with an extended base and long anterior rays. Caudal fin hemiheterocercal.

Type (and only) species. *Ischnolepis bancrofti* Haughton.

Remarks. *Ischnolepis* is probably the earliest known redfieldiiform genus. This new description was made possible only after preparation of specimens in the British Museum (Natural History) using an ultrasonic probe—a remarkably sensitive tool in certain circumstances (Macadie 1967).

Ischnolepis is similar to members of many palaeonisciform families, but it already displays characters which are diagnostic of the family Brookvaliidae, such as a narrow crescent-shaped dermosphenotic and an opercular series which includes a single branchiostegal ray.

Ischnolepis bancrofti Haughton

(Figs 1–6)

1934 *Ischnolepis bancrofti* Haughton: 97–101, text-figs 1–2, pl. 29.

Horizon and locality. Upper Permian or Scythian. Madumabisa shales, 82 miles from Kabwe (Broken Hill), Lunsempfwa Valley, Zambia.

Diagnosis. As for the genus *Ischnolepis*.

Holotype. S.A.M. 9338 with counterpart S.A.M. 9339.

Material. Photographs of holotype, P.27577–9.

The material in the B.M.(N.H.) consists of two blocks (part and counterpart; P.27577–8) and several fragments (collectively P.27579); all contain specimens of *Ischnolepis* together with an unidentified palaeoniscoid.

Description. *Size* (Fig. 1). The total length from snout tip to the posterior end of the caudal fin in the most complete specimen is 62 mm. The body is fusiform.

Skull (Fig. 2). The overall shape of the skull is very similar to that of *Brookvalia;* it is bullet-shaped and its main features are a large orbit, a moderately oblique opercular series and a slender, curved lower jaw. Almost all the skull bones are ornamented with rugae.

The suprascapular is ornamented with a few tubercles and with elongate rugae which radiate from its antero-dorsal corner. In a specimen on block P.27578, the inner surface of the dermopterotic bears a ventral lamina which runs close to the ventral border of the bone. The posterior end of this lamina appears to be in close association with the dorsal tip of the ascending process of the parasphenoid.

Dorsal to the dermopterotic there are two parietals, the posterior of which is triangular and small, and usually poorly preserved. The anterior extent of the anterior parietal is marked only by a ridge seen in a specimen on block P.27577 (Fig. 3). There is no sign of any extension of the supraorbital canal onto the parietal. The anterior end of the dermosphenotic is very narrow and appears to converge to a point, although its extreme tip is not preserved. Its ventral border is ornamented with four ridges which consist of rows of closely associated rugae. The relationship between the dermosphenotic and the postorbital and suborbital bones is not clear (Fig. 3), the skull roof, including the dermosphenotic, being displaced relative to the cheek bones. In my restoration (Fig. 2) the dermosphenotic has been

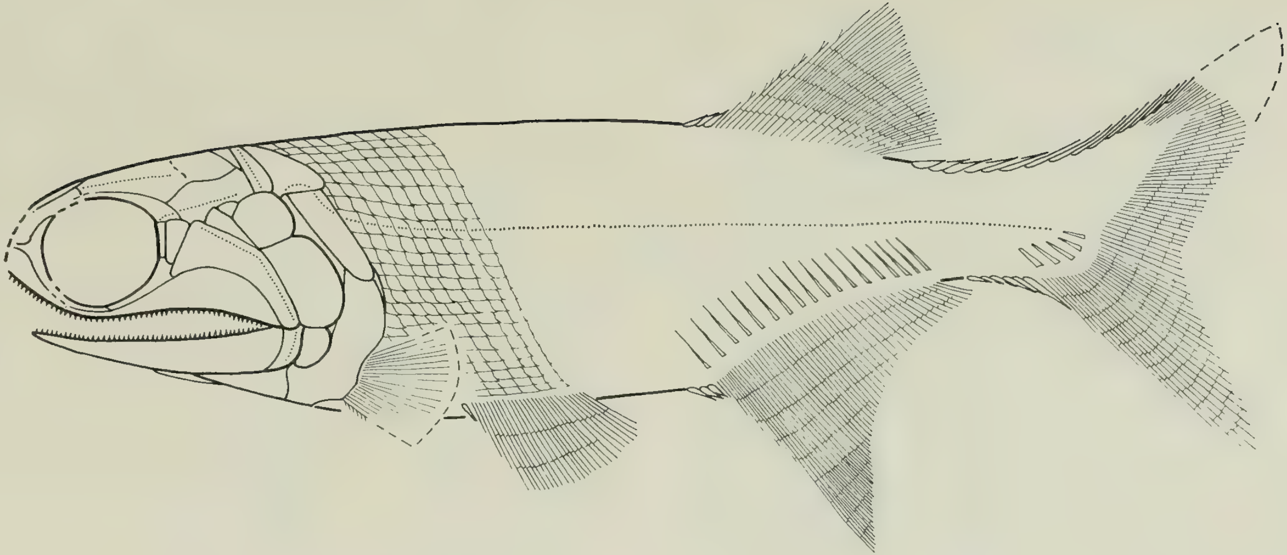

FIG. 1. *Ischnolepis bancrofti* Haughton. Restoration, ×2·5 approx. Posterior scales omitted.

drawn so that its ventral edge continues the curve of the orbit border suggested by the anterior margin of the postorbital.

There is only one branchiostegal. Several specimens were prepared to reveal the ventral side of the pectoral girdle and the lower jaws. During this preparation, delicate bones of the gill arch system were revealed, and if branchiostegals had been present it is likely that they would have been seen. Schaeffer's opinion (1967 : 334) that *Ischnolepis* lacks a complete branchiostegal series is thus confirmed. Haughton (1934 : 99) observed branchiostegals in *Ischnolepis*, but only in a single fragment; in this context it is significant that mixed with the specimens of *Ischnolepis* there are specimens of a palaeoniscoid, of similar size and proportions, which have eight pairs of branchiostegal rays.

The anterior edge of the subopercular lies at 65° to the ventral margin of the maxilla; the orientation of the opercular series is thus almost identical to that of *Brookvalia.* The ornament on the subopercular varies from small tubercles to elongate rugae which radiate from a point about a third of the way down the anterior edge. As well as rugae, the subopercular bears faint concentric ridges which run parallel with its posterior border; these are probably the result of uneven growth.

In a specimen on block P.27578, and less clearly in one on block P.27577, there is a single plate-like diamond-shaped bone, which lies ventral to the lower jaw ramus.

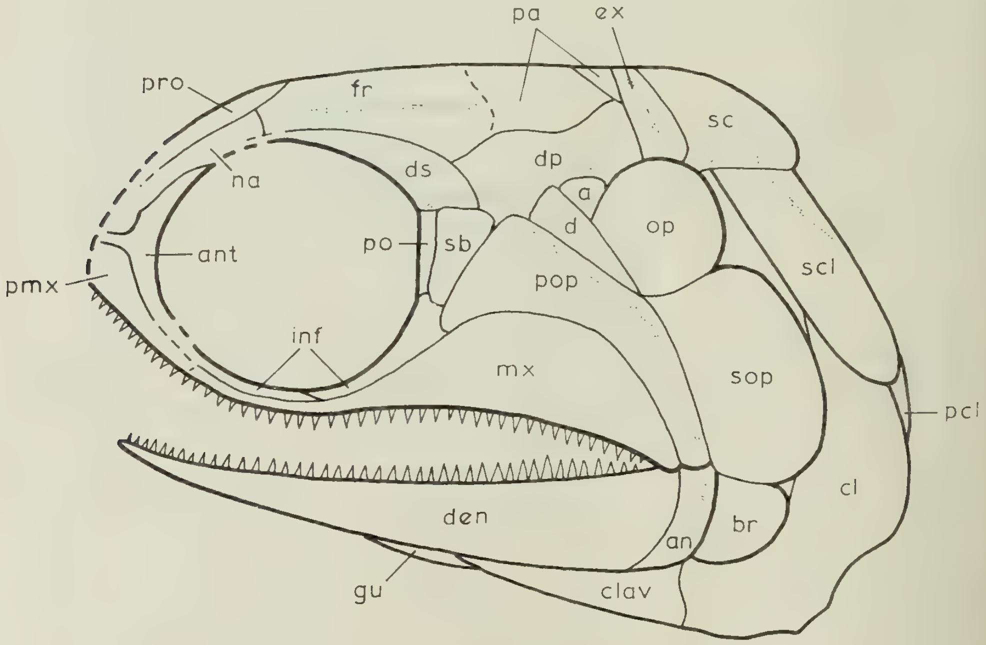

Fig. 2. *Ischnolepis bancrofti* Haughton. Restoration of skull and pectoral girdle, ×5·5 approx.

There are faint traces of grooves running parallel to its anterior margins. Although damaged, this bone appears to have been bilaterally symmetrical, and is therefore a mid-line element; probably a median gular.

In a specimen on block P.27577, a fragment of the right dermohyal is fused, or at least is in close contact, with the underlying hyomandibular. There is a tiny element lying ventral to the dermohyal, inserted between the antero-dorsal corner of the subopercular and the posterior margin of the preopercular. This element corresponds with the accessory opercular recorded in many palaeoniscoids (e.g. *Watsonichthys*, Gardiner 1963). It is seen only on the medial surface of the cheek (Fig. 3), laterally it is covered by the antero-dorsal corner of the opercular.

The preopercular has similar proportions to that of *Brookvalia*, except that its anterior limb extends antero-ventrally for a short distance dorsal to the antero-dorsal border of the maxilla. Along the posterior part of the suture between the preopercular and the maxilla there is a very shallow medial lamina on the preopercular which underlaps the maxilla (Fig. 3). Further anteriorly there is a groove in the antero-dorsal edge of the maxilla which receives the antero-ventral part of the preopercular. Ornament on the maxilla consists of tubercles and some elongate rugae which radiate from the point on its ventral margin which lies below the posterior edge of the orbit. The posterior infraorbital is expanded posteriorly and has a complex postero-dorsal edge: it butts against the postorbital and the antero-ventral tip of the preopercular and, between these two contacts, is notched to receive

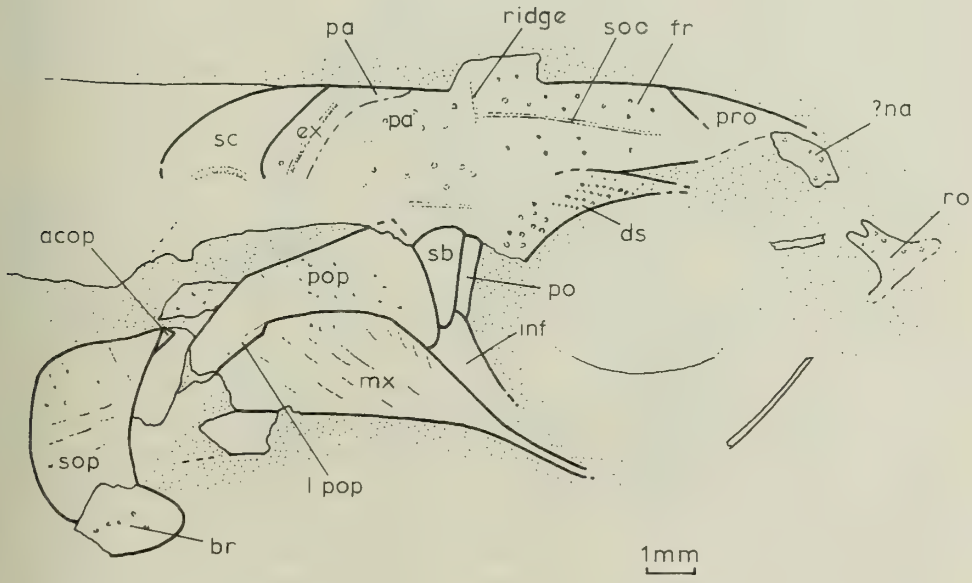

Fig. 3. *Ischnolepis bancrofti* Haughton. P.27577: cheek, left side internal view; roof, impression of left side.

the ventral tip of the suborbital. The anterior infraorbital extends along the ventral border of the orbit and is extremely narrow and, as at this same point the maxilla is narrow, the infraorbital bar is very slender.

The snout is poorly preserved. In a specimen on block P.27578, there is a fragment of bone sutured to the anterior end of the left frontal which is probably part of the nasal. A narrow curved fragment seen in a specimen on block P.27577 (Fig. 3) is probably also nasal. Neither of these fragments gives any indication of the anterior extent of this bone. A postrostral is preserved in the specimen noted above (on P.27578). It is lozenge-shaped, smooth and has a peg-like extension at its anterior end. A poorly preserved rostral (on P.27577, Fig. 3) bears a notch which probably accommodated this peg.

There is clear evidence of only one other bone in the snout region. This is a narrow curved antorbital which borders the anterior margin of the orbit. Midway along its anterior edge there is an anterior process. It is not certain whether a premaxilla is present, although in a specimen on block P.27577, an elongate tooth-bearing element is seen lying medial to the anterior end of the right maxilla. Anteriorly this element is expanded and it is thus unlikely to be entirely composed of maxilla. Comparison with *Brookvalia* suggests that it is premaxilla, but the possibility that it is partly rostral or a rostro-premaxilla must be admitted.

Lower Jaw (Fig. 4). The lower jaw is deep posteriorly and tapers towards the symphysis so that the anterior part is very slender. The dentary is a thin lamina of bone ornamented with elongate rugae. It bears conical teeth which are 0·5 mm high. Halfway up each tooth there is a slight constriction above which the profile is somewhat bulbous. In lateral view the profile is asymmetrical, the tip being slightly recurved (Fig. 4). In a specimen on block P.27578, broken teeth show that the outer enamel layer is about 0·03 mm thick. Only posterior teeth are preserved. They are closely spaced, and it is estimated that there were as many as 50 on the dentary.

The meckelian bone extends along the entire length of the medial side of the lower jaw. Anteriorly, where it is best preserved, it has a round cross-section. There is a narrow element, also round in cross-section, running immediately below the meckelian bone. Comparison with *Pteronisculus* (Nielsen 1942) suggests that, for most of its length at least, this is part of the dentary and consists of a tube enclosing the mandibular canal. In *Ischnolepis* this structure is only 0·3 mm deep in side view and it was not possible to ascertain whether or not it contained a canal. Above the meckelian bone there is an indeterminate number of coronoid elements. It is not known to what extent these thin bones overlapped the meckelian bone on its medial side. The internal edges of the internal lamina of each coronoid bear low conical teeth which are about 0·15 mm high. It is estimated that there were originally about 50 of these teeth along the length of the lower jaw. In addition, 9 small teeth are situated on the posterior coronoid (or the posterior part of the posterior coronoid) which slopes postero-dorsally close to the jaw articulation. Numerous extremely small teeth are scattered on the surface of the internal lamina of the coronoids.

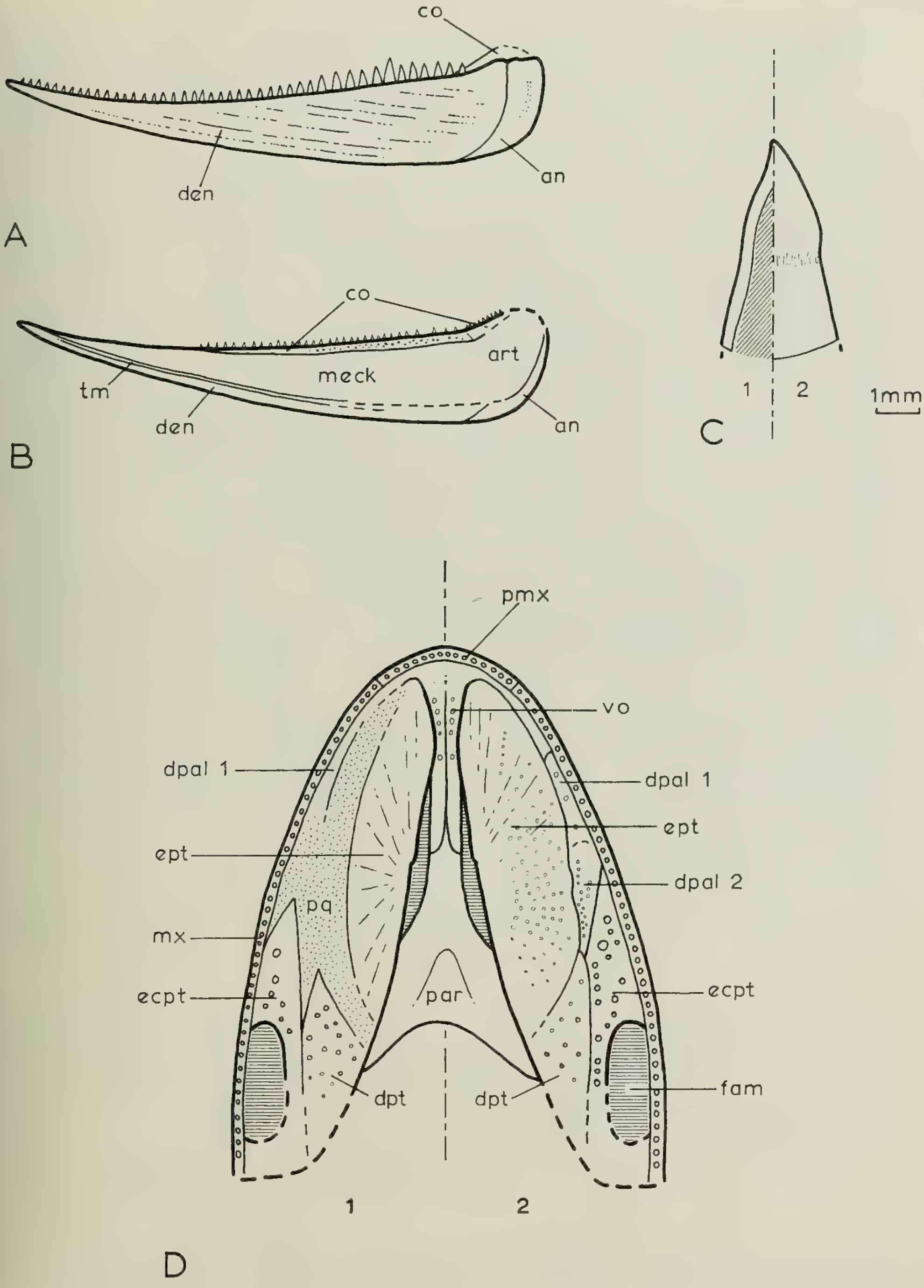
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FIG. 4. *Ischnolepis bancrofti* Haughton. (A) Lower jaw. Restoration of right ramus in lateral view, coronoid teeth omitted, ×5·5 approx. (B) Lower jaw. Restoration of left ramus in medial view, dentary teeth omitted, ×5·5 approx. (C) Dentary tooth from P.27578: 1, in section; 2, in lateral view. (D) Restoration of palate in ventral view, ×5·5 approx.; 1, incompletely ossified; 2, completely ossified.

Palate. The palatoquadrate complex is preserved in several specimens. In one (on block P.27577) growth of the dermal bones associated with the palatoquadrate is incomplete, whereas in others the palate has a complete covering of dermal bones (Fig. 4). The dermal bones associated with the palatoquadrate have been restored in ventral view (Fig. 4). The endopterygoid is the main anterior element. Its centre of ossification lies almost halfway along the medial border of the palatoquadrate. Rows of tiny teeth radiate from this centre of ossification. An unusual feature of the palate is that the endopterygoid is completely separated from the ectopterygoid by a junction of the posterior dermopalatine and the dermometapterygoid. The dermometapterygoid is comparable in size with the endopterygoid, and forms the major part of the postero-dorsal surface of the palate.

The lateral edge of the endopterygoid is bounded by two dermopalatine elements, the anterior of which is narrow and bears a single row of teeth. The posterior dermopalatine is slightly broader and bears three rows of small teeth running parallel to the long axis of the bone. Posterior to the dermopalatines there is a broad ectopterygoid, which extends posteriorly as a narrow strip running alongside the lateral border of the dermometapterygoid. The ectopterygoid bears several rows of teeth, those in the centre row being comparable in size with those of the dentary.

The toothless parasphenoid extends between the anterior part of the palatoquadrates, but its relationship with the snout is unknown. Posteriorly it bifurcates so that its overall shape corresponds to an inverted Y. The major part of the posterior half of the parasphenoid consists of the two ascending processes. These are narrow and elongate and appear to extend to the lateral walls of the skull for, in a specimen on block P.27578, the distal end of the left ascending process appears to meet the posterior part of an internal lamina running along the inside of the dermopterotic, implying that a spiracular canal was present, as in *Pteronisculus*. The basipterygoid process is much smaller than the ascending process and is composed of a ventral fold of the lateral edge of the parasphenoid. There is an oval dome on

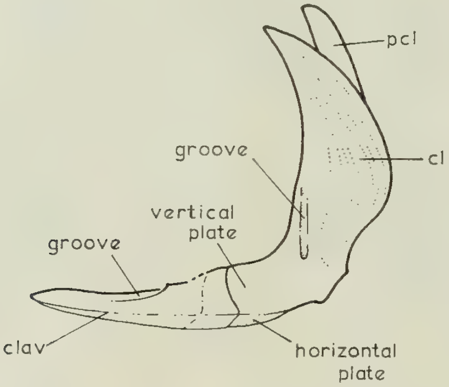

FIG. 5. *Ischnolepis bancrofti* Haughton. Restoration of dermal bones of left pectoral girdle, ×4·5 approx. Ornament on cleithrum restored from internal surface.

the ventral side of the centre of the posterior part of the parasphenoid. The function of this dome is unknown. Its position corresponds with that of a depression seen on the dorsal side of the parasphenoid in *Pteronisculus* (Nielsen 1942).

There are two narrow vomers ventral to the lateral edges of the anterior part of the parasphenoid. In a specimen on block P.27578 a short midline suture is seen at the anterior end of the parasphenoid, which suggests that the vomers met one another, at least anteriorly. The vomers, unlike the parasphenoid, bear small teeth.

Pectoral girdle. The ventral part of the pectoral girdle is restored in lateral view in Fig. 5. The supracleithrum is almost as wide as the ventral part of the suprascapular against which it butts. Ornament on the medial surface of the supracleithrum consists of grooves which run parallel to the long axis of the bone; a row of tiny tubercles runs along the bottom of each of these grooves. These are evenly spaced and number about 30 per mm. Only the postero-dorsal corner of the supracleithrum has a smooth surface.

The cleithrum bears a shallow groove on its lateral surface. Its medial surface is ornamented with very fine grooves which bear rows of tiny tubercles similar to those described on the inner surface of the supracleithrum. The anterior margin is devoid of any ornament.

The clavicle is narrow in lateral view, tapering to a point anteriorly; posteriorly it forms a broad lamina which overlaps the anterior end of the vertical plate of the cleithrum. Between this posterior lamina and the anterior half of the clavicle there is a groove which opens anteriorly, and extends posteriorly on the medial side of the posterior lamina. The clavicles appear to have met one another along almost their entire length.

Fins. The fins of *Ischnolepis* are well preserved, and a fairly complete account of their structure can be given. This description differs from that of Haughton (1934 : 97) mainly in that fringing fulcra are described only on the anterior rays of the pectoral fin, and less certainly on the dorsal fin. Several other fins with fringing fulcra are preserved in specimens P.27577 and P.27578, but these are associated with body fragments which cannot be assigned to *Ischnolepis* with certainty. As there is at least one other palaeoniscoid preserved with *Ischnolepis*, confusion could easily result from a description of any material with uncertain affinities, and information from doubtful specimens has not been used here.

Paired fins. The pectoral fin has 20 rays. The anterior ray has a base considerably broader than those of its fellows and bears fringing fulcra. Neither jointing, nor distal bifurcation was observed in any ray. The five anterior rays are associated with a single distal radial, and the two following rays with a second. The proximal ends of the other rays are not seen. The preservation of the pectoral fin in a specimen on block P.27577 suggests very strongly that its base, and therefore also the margo radialis, was orientated vertically.

The pelvic fin has a long base, so it is almost rectangular in shape. There are 29 rays which have 2 joints.

Unpaired fins. The anal fin is very large. Its base is 20% of the total body length. There are 51 rays, and as the anterior rays are six to seven times as long as the

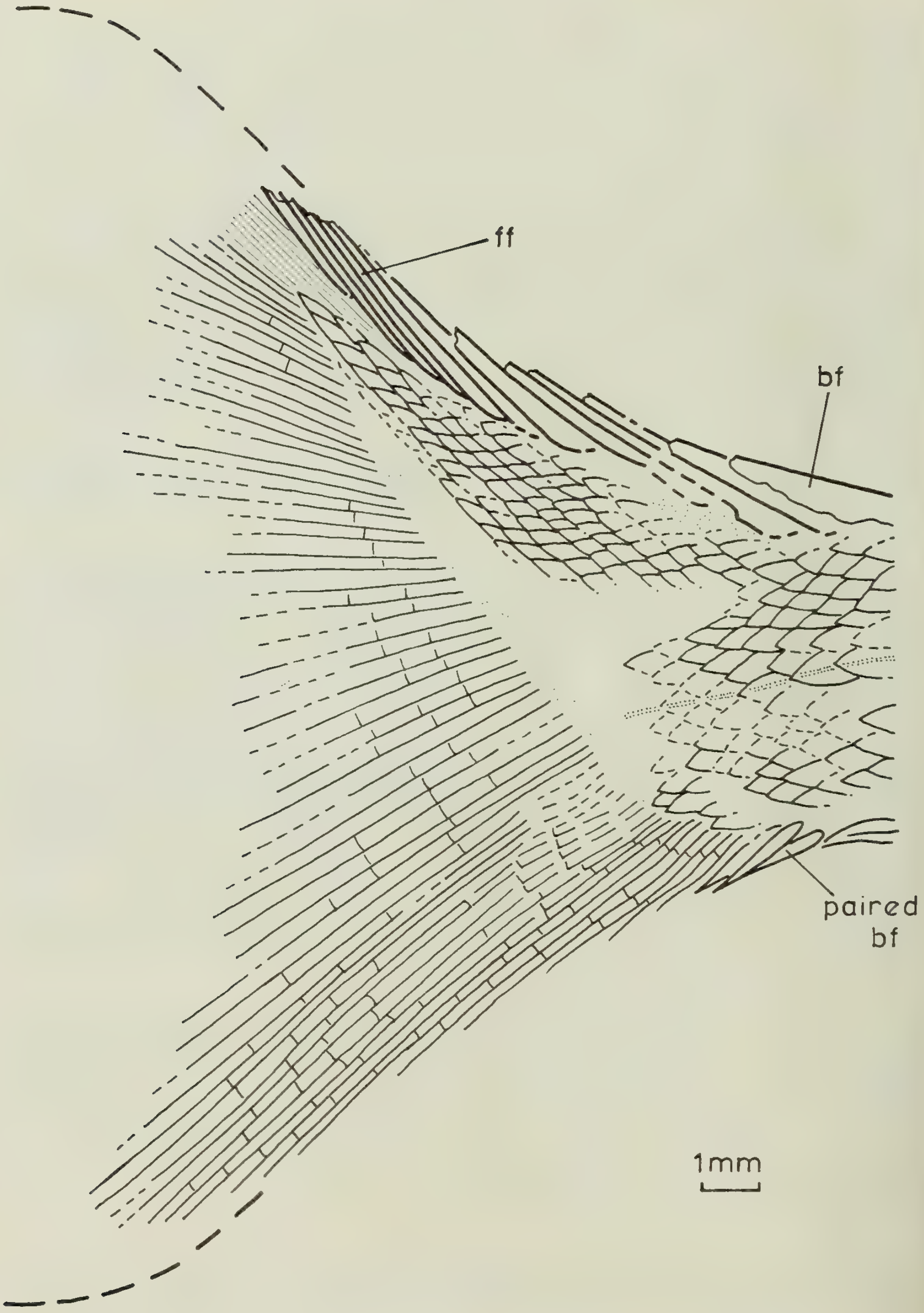
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FIG. 6. *Ischnolepis bancrofti* Haughton. Caudal fin, P.27577. Right side.

posterior rays, the fin has an overall triangular appearance. The anterior rays have 8 joints and bifurcate distally, the posterior rays have as few as 2 joints and do not bifurcate.

The dorsal fin has 26 rays which have 5 joints, and which are bifurcated along almost their entire length. In some specimens there are faint traces of fringing fulcra on one of the anterior rays.

The caudal fin is well preserved except for the tip of the dorsal lobe (specimen in block P.27577, Fig. 6). Photographs of the holotype (S.A.M.9338) show that the lobes are equal in size and that the fin is not deeply cleft. The body lobe is long, extending over halfway along the length of the dorsal lobe. There are 66 rays; those of the dorsal lobe have 3 joints, and those of the ventral lobe up to 11 joints. The 7 anterior rays of the dorsal lobe are epaxial in position. Distal bifurcation was not observed in the specimens available for study, although this has been noted in the holotype (Haughton 1934 : 101).

Squamation. The scales are leaf-shaped, the largest flank scales being 0·8 mm long and 0·7 mm deep. They bear an ornament consisting of a row of closely spaced tubercles which form a ridge running postero-ventrally across each scale. There are 50 body transverse scale rows, containing about 30 scales in the region of the dorsal fin. The change in orientation of scales from body to body lobe is achieved gradually, so that there is no hinge line visible at the base of the body lobe.

Genus *ATOPOCEPHALA* Brough 1934

1934 *Atopocephala* Brough: 564.

Diagnosis (emended). Head bluntly pointed. Skull bones ornamented with tubercles. One pair of parietals. Dermopterotic short and deep. Frontal elongate, separated from the orbit edge by dermosphenotic. Snout region poorly known, but appearing to be similar to that of *Brookvalia*. Opercular series almost vertical. Opercular and subopercular of almost equal size, and bearing long spines projecting from their posterior borders. Antopercular with curved posterior border. A single suborbital present. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth pointed and slightly recurved. Lower jaw deep posteriorly, tapering abruptly anteriorly. Lower jaw shorter than the upper jaw margin.

Body fusiform. Pectoral girdle ornamented with tubercles and parallel ridges. Scales rhombic and ornamented with tubercles. Jointing regular on all fin-rays, except the anterior rays of the pectoral fin which are unjointed. Fin-rays with large fulcra. Caudal fin hemiheterocercal and equilobate.

Type (and only) species. *Atopocephala watsoni* Brough.

Remarks. *Atopocephala*, although a member of the family Brookvaliidae, obviously represents a line which is separate from what may be regarded as typical members of the family—*Ischnolepis* and *Brookvalia*. The main feature of the genus is the shortness of the skull. As a result of this, the skull bones are relatively deeper than those of other brookvaliid genera, although the actual interrelationships of the bones remain unchanged.

Atopocephala watsoni Brough
(Fig. 7)

1934 *Atopocephala watsoni* Brough: 564–570, text-figs 2–3, pl. 1, figs 2–3.

Horizon and locality. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis. As for the genus *Atopocephala*.

Holotype. P.16079–80. A specimen with counterpart, the only specimen known.

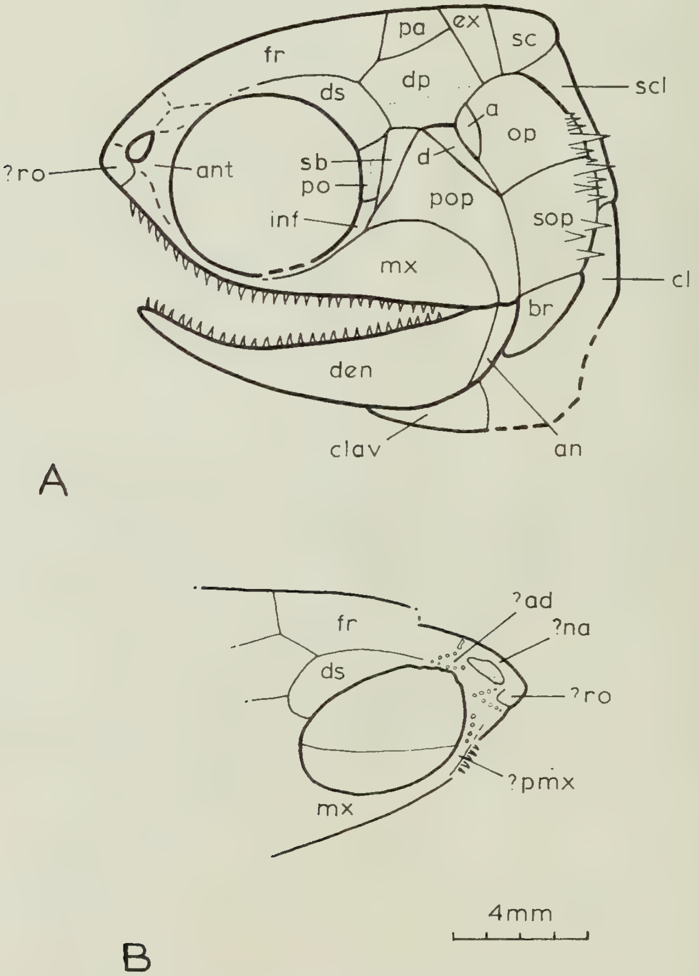
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Fig. 7. *Atopocephala watsoni* Brough. (A) Restoration of skull and pectoral girdle, ×4·5 approx. (B) P.16080, impression of left side.

Description. The only additions to the description given by Brough (1934 : 564) are a new interpretation of the snout and of the opercular region (Fig. 7).

The snout region is difficult to interpret. The only certain features are the nostril outline, a suture running from the antero-ventral corner of the nostril to the edge of the snout and the presence of a toothed element on the ventral edge of the snout. The only other indications of the probable pattern of the bones of the snout consist of rows of tubercles. These are almost confluent, and form elongate rugae which may mark the outlines of elements (Fig. 7). The area occupied by the nasal in Brough's figure (1934 : text-fig. 3), contains two elements which are here interpreted as being the adnasal and antorbital. The anterior border of the orbit is formed by the antorbital. This element is separated from the ventral edge of the snout by a narrow (?) premaxilla. Dorsal to the top part of the antorbital there is a diamond-shaped adnasal which just borders the nostril anteriorly and the dermosphenotic posteriorly. The dorsal edge of the nostril is bordered by the nasal, a rectangular element which meets the frontal posteriorly and the rostral anteriorly. There is no postrostral.

Anterior to the opercular there is an antopercular and a dermohyal. The dermohyal is elongate and extends ventrally to the antero-ventral corner of the opercular. The antopercular has a curved posterior margin which fits into a notch in the antero-dorsal corner of the opercular (see Brough 1934 : pl. 1, fig. 3).

A suture between the angular and the dentary is clearly visible.

Genus ***BROOKVALIA*** Wade 1933

1933 *Brookvalia* Wade: 121
1935 *Brookvalia* Wade; Wade: 20
1935 *Dictyopleurichthys* Wade; Wade: 35
1935 *Beaconia* Wade; Wade: 33

Diagnosis (emended). Head bullet-shaped with large orbit anteriorly placed. Skull bones ornamented with tubercles. Posterior parietal triangular. Dermopterotic extensive dorsally and bearing a posterior extension of the supraorbital sensory canal. Frontal curved and elongate, bordering, or almost bordering, part of the dorsal edge of the orbit. Small rostral element at snout tip, probably bordering the anterior edge of the nostril. Opercular series narrow and moderately oblique. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth sharp, conical and numerous. Lower jaw with slight dorsal curve toward the symphysis. Lower jaw shorter than upper jaw margin.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped and ornamented with rugae. Jointing regular on all fin-rays except those of the pectoral fin, in which jointing only occurs distally on the anterior rays. Caudal fin hemiheterocercal and equilobate.

Type species. *Brookvalia gracilis* Wade.

Remarks. In this revision, five species classified in three genera by Wade (1935) have been reduced to four species, all included in a single genus. *B. parvisquamata* has been made a junior synonym of *B. gracilis* and *Dictyopleurichthys* *latipennis* has been included in the genus *Brookvalia*, but retains its identity at the species level because of its slightly different scale ornament. Finally, the identification of an antopercular and of a single branchiostegal in *Beaconia* makes the validity of that genus extremely doubtful, and the one species which it contained has been removed to the genus *Brookvalia*.

The members of *Brookvalia* as here constituted differ significantly from one another only in their overall body shape, in the shape of the caudal fin and in the size, shape and position of the dorsal fin.

Brookvalia gracilis Wade

(Figs 8–12, 14)

1933 *Brookvalia gracilis* Wade: 121–123, text-fig. 1.
1933 *Brookvalia parvisquamata* Wade: 124–125, text-fig. 3.
1935 *Brookvalia gracilis* Wade; Wade: 21–29, text-figs 5–14, pl. 4, fig. 1, pl. 5, fig. 1.
1935 *Brookvalia parvisquamata* Wade; Wade: 31–33, text-fig. 16, pl. 5, fig. 2.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis (emended). Extrascapular pentagonal. Two pairs of parietals, posterior element triangular, anterior element roughly oval and bearing two short parallel sensory canals. Dermopterotic bearing a short posterior extension of the supraorbital sensory canal. Postrostal probably present. Infraorbital elements reduced so that maxilla probably borders ventral edge of the orbit. Enlarged recurved teeth at tip of lower jaw.

Body slender. Scales ornamented with single, or rarely two, elongate rugae. Fringing fulcra not numerous, but present on anterior rays of all fins. Pectoral and pelvic fins equal in size, and fan-shaped with anterior and posterior rays almost equal in length. Dorsal fin originating just anterior to anal fin. Caudal fin deeply forked, with a few bifurcated rays in the lower lobe.

Holotype. P.15799 and counterpart P.15800.

Material. Holotype and P.15801–11, P.15813–24, P.15826–33, P.15835–42, P.15844–51, P.15853–6, P.15858, P.15860, P.15872, P.15878–9, P.15905–6, P.15914–5, P.15926, P.15930–1, P.15937, P.15939, P.15942, P.16997–17001, P.17005–17, P.24710–35.

U.S.G.D. 2, 4, 19, 28–9, 40–2, 80, 94, 141, 152, 159, 185–7, 205, 214, 218–19, 238, 244, 269, 272, 274, 277, 350 (at the University Museum of Zoology, Cambridge).

D.M.S.W. 383–8, 390–1 (at the University Museum of Zoology, Cambridge).

F.455 (at the Sedgwick Museum, Cambridge).

L.12143A–G.

Description. *Size* (Fig. 8). The total length from snout tip to the posterior end of the caudal fin varies from 30 mm (P.15810) to 125 mm (U.M.Z.C. uncatalogued). The body is fusiform and slender, its greatest depth occurring just behind the pectoral region.

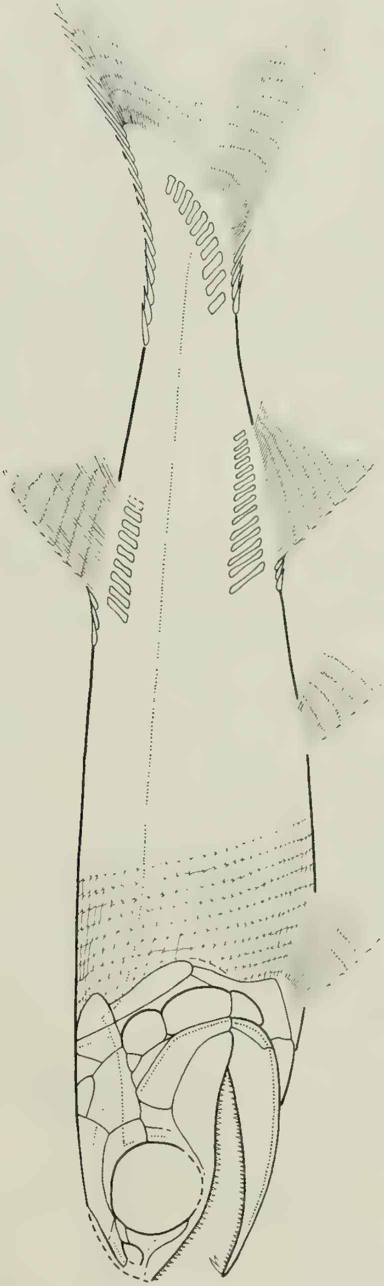

FIG. 8. *Brookvalia gracilis* Wade. Restoration, ×3 approx. Posterior scales omitted.

Skull (Fig. 9). The frontal is elongate, wide posteriorly and tapering towards the snout. It is sparsely covered with small tubercles. There are two pairs of parietals (parietal and postparietal of Wade). The anterior parietal is roughly oval, and bears three short rows of tubercles between which there were probably a pair of short sensory canals (U.S.G.D. 218 and P.15813, Fig. 10). The posterior parietal is larger than the anterior parietal and is triangular, coming to a point ventrally. In lateral aspect this element is small, but its dorsal extent is in fact quite large. It bears small tubercles. The dermopterotic is extensive, forming the main lateral element of the skull roof; it too bears tubercles.

The dermosphenotic is crescent-shaped and borders the postero-dorsal part of the orbit. Anteriorly it tapers to a point, but whether or not it meets the adnasal cannot be determined. It is thus possible that a small part of the frontal borders the dorsal edge of the orbit, though this is rather unlikely (see P.24730, Fig. 12).

In Wade's reconstruction of *B. gracilis* (1935 : text-fig. 5) the opercular lies ventral to the suprascapular and the extrascapular (post-temporal and tabular of Wade). This reconstruction is the result of misinterpretation of specimens in which opposite sides of the skull have been relatively displaced. In fact the opercular lies further anteriorly than in Wade's reconstruction with the result that the skull appears shorter, and the inferred angle of the suspensorium appears steeper (P.15813, Fig. 10). The opercular is oval and slightly longer than broad. It bears a series of low concentric ridges which follow the outline of the bone. The subopercular is elongate, being 1·5 times as deep as, and slightly longer than, the opercular. It

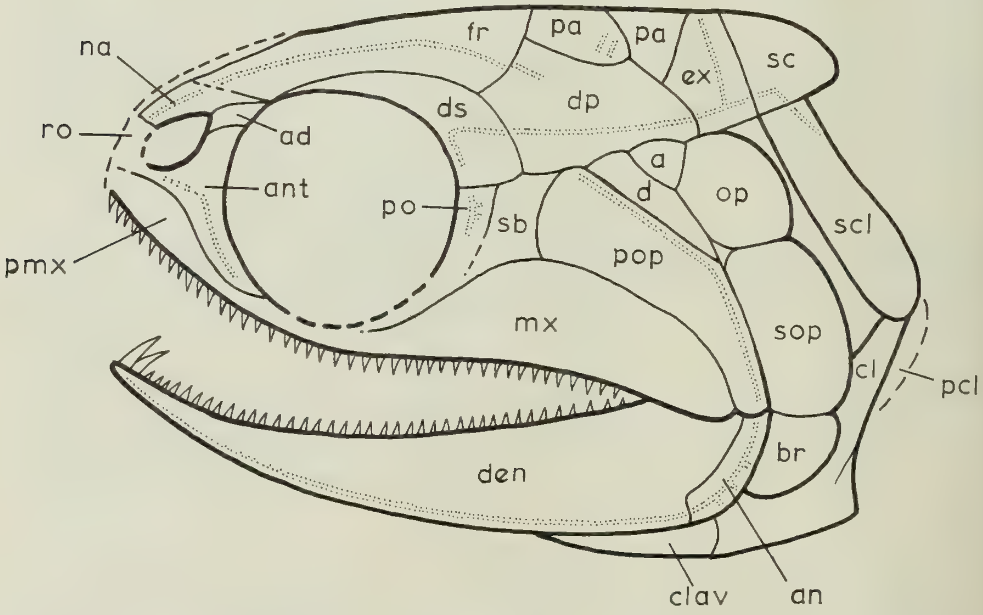

FIG. 9. *Brookvalia gracilis* Wade. Restoration of skull and pectoral girdle, ×5·5 approx.

bears a similar series of concentric ridges. The anterior edge of the subopercular lies at about 65° to the ventral margin of the maxilla. There is a single triangular branchiostegal element which is half as long as the supobercular. Together, the opercular bones form a shallow crescent.

Anterior to the opercular there is an antopercular and a dermohyal. The dermohyal is wedge-shaped and extends along the whole anterior edge of the opercular. It bears elongate rugae which run parallel to its long axis (P.24723).

The preopercular is definitely not as deep as indicated by Wade (1935 : text-fig. 5); its shape is clearly seen in a disarticulated specimen (P.24734). The maxilla is characterized by a long curved anterior extension which appears to border the ventral edge of the orbit for a short distance, although no specimen shows this area clearly. It bears about 35 sharp conical teeth which are up to 1 mm high in large specimens (e.g. P.15813, Fig. 10). The maxilla is ornamented with elongate ridges (U.M.Z.C. uncatalogued).

The postorbital region is rarely well preserved, but specimen P.24734 shows

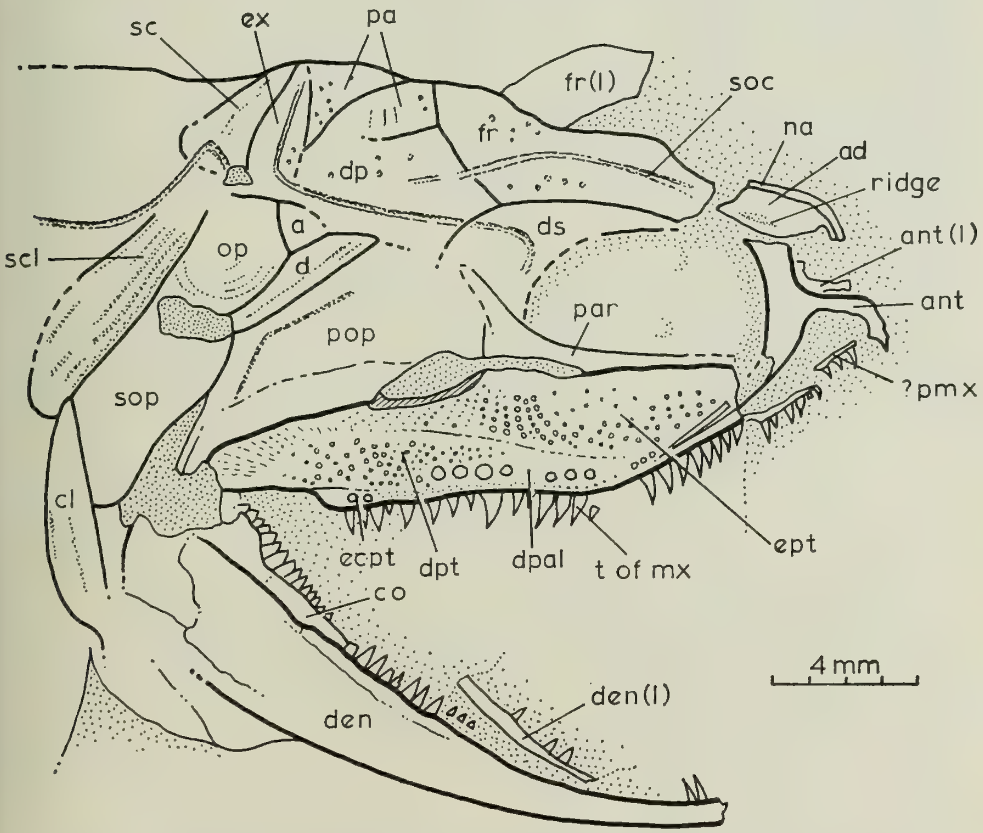

FIG. 10. *Brookvalia gracilis* Wade. P.15813: right side unless otherwise indicated.

that the preopercular was separated from the postorbital by a single element.

The snout is badly crushed in all specimens, but most of the elements can be identified with a high degree of confidence. The anterior edge of the orbit is bordered by two elements (P.15813, Fig. 10). The antorbital is the larger, more ventral of these elements, and is a long curved bone which sutures obliquely with the maxilla. Midway along its anterior border there is an anterior extension, which carries the infraorbital sensory canal forwards, and which borders the ventral edge of the nostril. This extension is similar to the rostral process described by Gardiner in the Lower Carboniferous palaeoniscoid *Nematoptychius greenocki* (1963 : 280). The anterior end of this extension is not preserved in *B. gracilis*. Dorsally, the antorbital meets the adnasal, a small diamond-shaped element which bears a single elongate ridge. The suture between the frontal and nasal is never very clear, but appears to be oblique, running antero-dorsally from near the orbit edge (P.24722). There is no evidence that the nasals met at the midline; they are always preserved as separate elements, and it is inferred that they, and possibly the anterior ends of the frontals, were separated by a median postrostral.

The upper jaw tooth row extends to the snout tip, but on an element which is quite separate from the antorbital (P.15813, Fig. 10). It would appear that fragmentation of the snout elements, as described by Gardiner (1963), has taken place, and that the ventral part of the snout in *B. gracilis* therefore consists of either a rostro-premaxillary or a premaxillary. Unfortunately no specimen of *B. gracilis* is well enough preserved to demonstrate which of these conditions is present, but comparison with *B. propennis* (Fig. 13) suggests that the rostral and premaxilla in *Brookvalia* are separate.

Lower jaw. The lower jaw (Fig. 11) is deep posteriorly and curves gently upwards towards the anterior end. The teeth on the anterior end of the dentary do not meet the most anterior teeth of the upper jaw. The dentary bears an ornament of strong longitudinal ridges. There are about 40 teeth which are sharply pointed and which appear in some specimens to curve very slightly posteriorly. In large specimens the teeth are 1 mm high, except for two or three teeth at the anterior

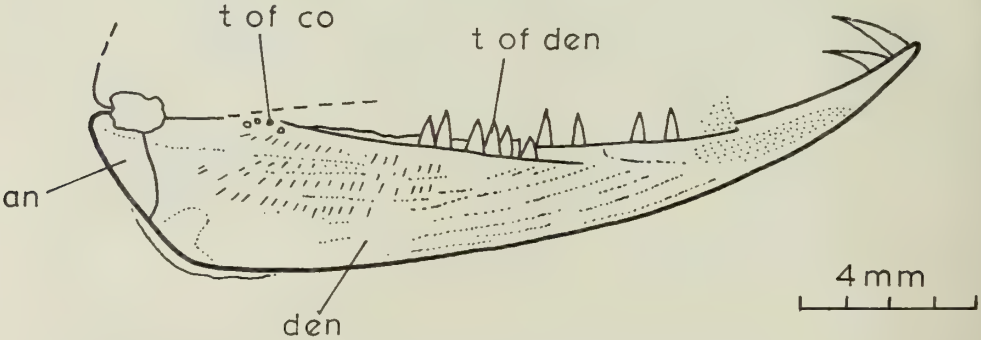

FIG. 11. *Brookvalia gracilis* Wade. P.15858: right side.

tip of the dentary which are twice as long as any other and which are sharply recurved (P.15858, Fig. 11). In lateral view the posterior coronoid curves dorsally along the dentary margin. This too bears numerous teeth which are up to 0·5 mm high, and which appear to overlap one another in lateral aspect (P.15813, Fig. 10).

Sensory canal system. Part of the ethmoid commissure is represented on the anterior process of the antorbital by two groups of three or four shallow pits, similar to those seen on the infraorbitals of *Aestuarichthys fulcratus* (Gardiner 1969 : 437). No trace can be seen of the anterior branch of the infraorbital sensory canal on the dermosphenotic figured by Wade (1935 : text-fig. 5). The supraorbital sensory canal is not of the normal palaeoniscoid pattern: it runs across the nasal and frontal, but posteriorly it passes onto the dermopterotic (Fig. 10). Often the canal is displaced slightly at the suture between the frontal and dermopterotic. In no specimen was the supraorbital canal observed to join the infraorbital canal on the dermopterotic (c.f. Wade 1935 : text-fig. 5). In some (e.g. P.15827 and P.24730, Fig. 12), there is apparent joining of the supraorbital and infraorbital canals, because canals from both sides of the skull are preserved and the canal which appears to run into a right infraorbital canal is in fact a left supraorbital canal. The left infraorbital canal is seen about a millimetre below the right infraorbital canal and the left supraorbital canal does not reach the latter (Fig. 12).

Palate. In specimens P.15827 and P.15813 (Fig. 10) the palate has been preserved. Its visible upper surfaces have been partly eroded away, revealing the roots of numerous teeth. The endopterygoid is wide anteriorly, and bears tiny teeth which

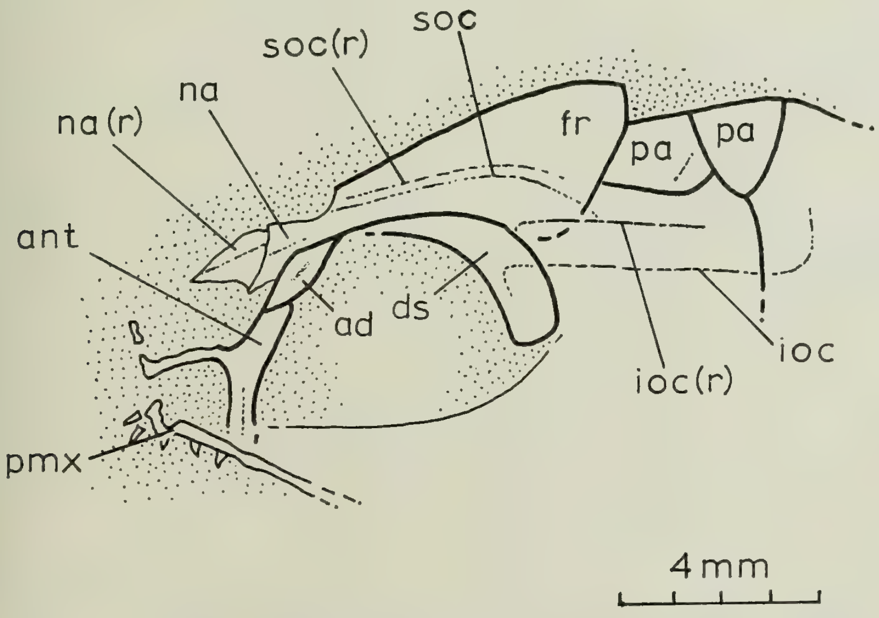

FIG. 12. *Brookvalia gracilis* Wade. P.24730: right side unless otherwise indicated.

are less than 0·1 mm in diameter, and which are arranged in rows which radiate from a point about halfway along its median edge. Lateral to the anterior edge of the endopterygoid is a dermopalatine element which is poorly preserved but which bears several teeth. Posterior to the dermopalatine is the ectopterygoid which bears numerous small teeth in addition to a row of six or seven larger ones. An area posterior to the ectopterygoid is very indistinct and presumably marks the position of the fossa for the adductor mandibulae. The dermometapterygoid sutures anteriorly with the ectopterygoid and endopterygoid. It bears numerous teeth which radiate from a point midway along its lateral border. Posteriorly there is a ridge and groove along the medial border of the palate; this was probably closely associated with the base of the hyomandibular. It is not clear whether this groove is in the endopterygoid or the dermometapterygoid.

Pectoral girdle. The supracleithrum is roughly oval in outline and extends ventrally to a point almost halfway down the posterior edge of the subopercular. It bears an ornament of three or four well developed concentric ridges (P.15827). The cleithrum is lanceolate dorsally, but wider ventrally. Just below the posterior margin of the lower jaw there is a clear suture between the cleithrum and clavicle (P.15853). The clavicle extends anteriorly below almost a third of the length of the lower jaw. Both the cleithrum and clavicle are ornamented with strong ridges. A postcleithrum is probably present, lying posterior to the dorsal half of the cleithrum (P.24713).

Paired fins. The pectoral fin has 17 rays (U.S.G.D. 269) which have one or two distal joints. The anterior ray supports fringing fulcra.

The pelvic fin has about 21 rays with up to 4 joints which are not limited to the distal parts of the ray (P.24722). The anterior ray supports fringing fulcra. Distal bifurcation was not observed in either the pectoral or the pelvic fins.

Unpaired fins. The anal fin has 42 rays which have up to 7 joints (P.25799). The anterior ray supports a few fringing fulcra. The dorsal fin lies slightly anterior to the level of the anal fin; the body transverse scale row which meets the anterior edge of the dorsal fin lies 9 scale rows posterior to the transverse scale row which meets the anterior edge of the anal fin. There are 32 rays, which have up to 6 joints (P.15799). The anterior ray bears fringing fulcra. Distal bifurcation was not observed in either the anal or dorsal fins.

In a study of the rhipidistian *Eusthenopteron foordi* (Thomson & Hahn 1968) it was demonstrated that there was a change in the relative size and position of the unpaired fins during the individual's life history. These changes implied changes in the fishes' habits. There is a large number of specimens of *B. gracilis* with a total length varying from 30 mm to 125 mm. In all these, the relative size and position of the unpaired fins remains constant, indicating that swimming habits remained constant during the life history.

In the adult, the heterocercal, equilobate caudal fin has up to 63 rays, a few of which in the ventral lobe bifurcate distally. Jointing is regular, and there are three joints in the dorsal lobe rays and up to 11 in the ventral lobe rays. The growth and development of the tail in *B. gracilis* is discussed below (see p. 328).

Fin skeleton. Young specimens of *B. gracilis* are incompletely scaled, and in some of these specimens parts of the fin skeletons are visible. Little detail can be made out, but it is clear that radial elements are fewer than the rays which they support. The anal fin has 14 radials which support 42 rays (P.15802), the dorsal fin at least 9 supporting 32 rays (P.15800) and the caudal fin at least 10, which extend along the ventral margin of the body lobe and support 33 rays.

Squamation. The scales are rhomboidal. They are exceptionally well preserved in specimen U.S.G.D. 218 (a specimen about 90 mm long) in which the largest scales are 0·8 mm long and 1 mm deep. There are 50 body transverse scale rows, containing about 30 scales in the region of the dorsal fin.

Each scale bears a ridge, or ruga, which bifurcates anteriorly, and which runs from the antero-dorsal to the postero-ventral corner of the scale. A few anterior flank scales bear two rugae.

Wade (1935 : 27) has described the gradual appearance of adult squamation in the growth series represented by large numbers of specimens of *B. gracilis.* In addition, it may be noted that young scales first appear as oblique 'scale buds': these approximate to the rugae seen in fully developed scales. In larger individuals the scales appear leaf-shaped, and it is only in the largest specimens that the scales fit closely together or overlap slightly, to give the appearance of a pattern of repeated rhomboidal shapes.

Brookvalia parvisquamata Wade

1933 *Brookvalia parvisquamata* Wade: 124–125, text-fig. 3.
1935 *Brookvalia parvisquamata* Wade; Wade: 31–33, text-fig. 16, pl. 5, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

HOLOTYPE. P.15798.

MATERIAL. Holotype and P.15843.

REMARKS. All the characters listed by Wade (1935 : 31) in his diagnosis of *B. parvisquamata* are found also in *B. gracilis.* In addition, all other characters that can be seen in *B. parvisquamata* (for example, the pattern of the sensory canals of the head) are also seen in *B. gracilis.* It is therefore proposed that *B. parvisquamata* is a junior synonym of *B. gracilis.*

Brookvalia propennis Wade

(Fig. 13)

1933 *Brookvalia propennis* Wade; 124, text-fig. 2.
1935 *Brookvalia propennis* Wade; Wade: 29–31, text-fig. 15, pl. 4, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS (emended). Skull incompletely known; discernible features as in *B. gracilis.*

Body slender, with caudal peduncle slightly deeper than in *B. gracilis*. Scales ornamented with two, or rarely three, elongate rugae. Fringing fulcra on anterior rays of all fins. No distal bifurcation in any fin-ray. Fins triangular with anterior rays 3–4 times as long as the posterior rays. Pectoral fin base 1·5 times as long as that of the pelvic fin, and composed of laterally expanded rays, with joints only at distal end of anterior rays. Anterior edge of dorsal fin lying just posterior to the level of the anterior edge of the pelvic fin. Caudal fin not deeply forked.

HOLOTYPE. U.S.G.D. 203.

MATERIAL. Holotype and P.15825 with counterpart P.15868, P.15850, P.24699 and P.24710.

DESCRIPTION. *Size.* The best preserved specimen of *B. propennis* is P.15825. Its length, measured from snout tip to the posterior end of the caudal fin, is 61 mm. The body is fusiform, its greatest depth occurring at the pectoral region. The body of *B propennis* is very similar to that of *B. gracilis* except that the caudal peduncle in the former species is slightly deeper.

Skull. The skull in all specimens is badly crushed and few sutures can be seen. The anterior parietal appears to be slightly larger than in most specimens of *B. gracilis*, but this is not very significant because the apparent size and shape of the parietals in *B. gracilis* was seen to depend considerably upon the mode of preservation of each specimen. The extrascapular extends slightly further anteriorly than in *B. gracilis*, but the other skull bones show no significant differences from that species: they are ornamented with a similar pattern of tubercles; an antopercular and a dermohyal are present (P.15850); the ventral margin of the maxilla has the same characteristic convex curve below the orbit, followed by an upward curve towards the snout.

The snout is badly crushed, but in specimens P.15825 and its counterpart P.15868 (Fig. 13) there are two short tooth-bearing elements which run to the snout tip, between which there is a triangular element which bears numerous tooth-like denticles. These elements can be identified as premaxillae and rostral respectively. The more dorsal snout elements cannot be identified with certainty.

The lower jaw is characterized by the upturned tip seen in *B. gracilis* and the teeth, where preserved, are sharp and conical.

Pectoral girdle. Only the cleithrum is preserved. It is slender ventrally and ornamented with elongate ridges.

Paired fins. The pectoral fin is triangular and has 19 rays which are very broad, being composed of a median spine with flat lateral extensions. There are faint signs of two or three distal joints on the anterior rays (P.15850) but the other rays are unjointed. The anterior ray bears numerous fringing fulcra, and there is no distal bifurcation. Although composed of fewer rays, the pectoral fin is as large as the dorsal fin, and its base is 1·5 times as long as that of the pelvic fin.

The pelvic fin lies rather closer to the anal fin than to the pectoral fin. It is small and triangular. There are 24 rays, which are flattened laterally in a similar way to those of the pectoral fin, though to a lesser extent. There are up to 4 joints evenly distributed along the rays. A few fringing fulcra may be present on the anterior ray (P.15850), but poor preservation does not allow certain identification. There is no distal bifurcation.

Unpaired fins. The rays of the unpaired fins are not expanded laterally to the extent seen in the paired fins. The anal fin is the same shape as, but larger than, the pelvic fin. It has 21 rays, which have up to 8 joints. Each joint of the anterior rays bears a single fringing fulcrum. There is no distal bifurcation.

The dorsal fin is almost the same shape and size as the anal fin, and lies completely in front of the anal fin. The body transverse scale row which meets the anterior ray of the dorsal fin, meets the anterior ray of the anal fin. There are 27 rays which have up to 7 joints. The anterior rays bear fringing fulcra and there is no distal bifurcation.

The caudal fin is equilobate but is not as deeply forked as it is in *B. gracilis.* The upper lobe has 28 rays, 7 of which are epaxial in position. The rays have up to 15 joints, and those bordering the anterior edges of the dorsal and ventral lobes bear fringing fulcra. There is no distal bifurcation. The posterior basal fulcrum on the dorsal side of the tail is inserted just anterior to the posterior tip of the body lobe. This condition is seen in *B. gracilis,* but only in juvenile (i.e. incompletely scaled) specimens.

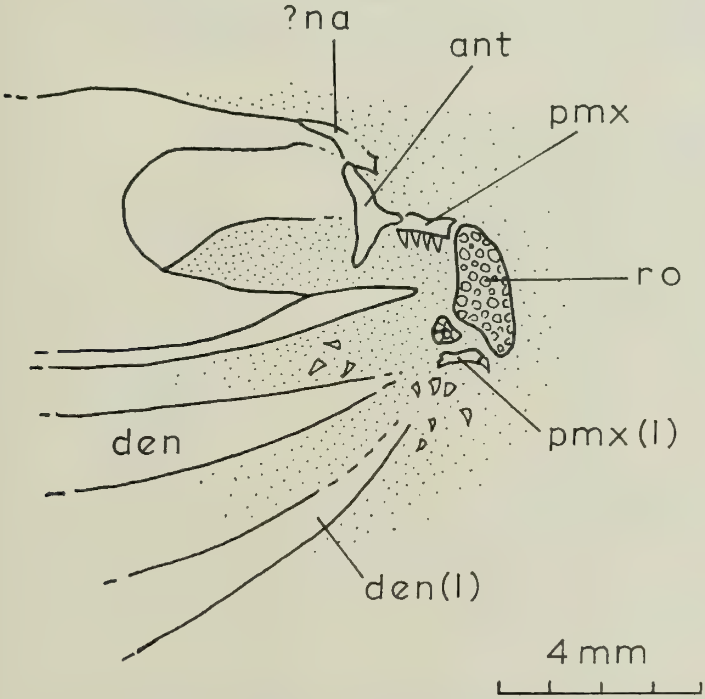

FIG. 13. *Brookvalia propennis* Wade. P.15868: right side unless otherwise indicated.

Squamation. The scales are leaf-shaped, but in the flank region they overlap and are rhomboidal in appearance. The largest scales are 0·8 mm long and 0·75 mm deep (P.15868) and are ornamented with two or more horizontal rugae. There are 40 body transverse scale rows, each calculated to contain up to 20 scales.

Brookvalia latipennis (Wade) comb. nov.

(Fig. 14)

1935 *Dictyopleurichthys latipennis* Wade: 35–37, pl. 7, fig. 1.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. Incompletely known. Discernible features as in *B. gracilis*, except that scales on the anterior flank region bear complex ornament of three or four rugae of variable length.

Holotype. P.15883, the only specimen known.

Remarks. *B. latipennis* is represented by a single fossil. The body is complete, but only the posterior part of the skull is present, and this is badly crushed so that sutures are not visible. The length of the body from the posterior edge of the pectoral girdle to the caudal peduncle is 65 mm.

Most of the characters listed by Wade in the generic diagnosis of *Dictyopleurichthys* (1935 : 35–36) occur also in the genus *Brookvalia*, these are:

1. The maxilla and dentary (posterior parts at least) are ornamented with elongate ridges.
2. The pectoral girdle is ornamented with elongate ridges.
3. The teeth are sharply pointed, and are 1 mm high.
4. The fins (the pectoral fin is not preserved) are the same shape and relative size, and are situated in the same positions as in *B. gracilis*.

In addition to the features noted by Wade, it is apparent that the fin-rays in *D. latipennis* and *B. gracilis* are similarly jointed, and the anterior rays in each case bear fringing fulcra. Also the numbers of fin-rays present compare closely with those known to be present in *B. gracilis:*

	B. gracilis	*D. latipennis*
Pelvic	21	at least 14
Anal	42	at least 40
Dorsal	32	at least 26
Caudal	63	at least 62

There are 48 body transverse scale rows, those in the pelvic region containing 32 scales. The scales are rhomboidal, or leaf-shaped where incompletely developed scales occur near the dorsal and ventral edges of the body.

Other characters listed by Wade in his description of *D. latipennis* would seem to be of little diagnostic significance:

1. Very few teeth are preserved, and not all show the lateral groove described by Wade. It is likely that this feature is the result of erosion of the tooth surface.

2. Wade (1935 : 36) describes the dorsal fin of *D. latipennis* as being ‘almost

completely anterior to the anal fin'. In fact, the anterior edge of the dorsal fin lies only 4 mm anterior to the level of the anal fin. The body transverse scale row which meets the anterior dorsal fin-ray lies 9 scale rows posterior to the row which meets the anterior ray of the anal fin; exactly the same condition is seen in *B. gracilis*.

3. The body is fusiform as in *B. gracilis*. The maximum body depth occurs immediately behind the pectoral girdle and measures 28 mm, which is over 25% of the estimated length between the snout tip and caudal peduncle. This implies that the body is deeper than in *B. gracilis*, in which the maximum body depth is just under 25% of the body length. This difference is not significant, however, because the ratio is variable in *B. gracilis* itself and, more importantly, the apparently increased depth may be due to compression during fossilization. The effect of compression is to exaggerate the body depth relative to body length in larger specimens, and *D. latipennis* is larger than any known specimen of *B. gracilis* (see Schaeffer, 1955 : 7–8 for a discussion of a similar situation).

The maximum body depth is 2·5 times the depth of the caudal peduncle, as is the case in *B. gracilis*.

4. As mentioned above, only the crushed remains of the posterior part of the head are preserved, and sutures are not visible. The following characters of the skull listed by Wade (1935 : 35) cannot be regarded as reliable:

1. Large orbits anteriorly placed.
2. Suspensorium moderately oblique.

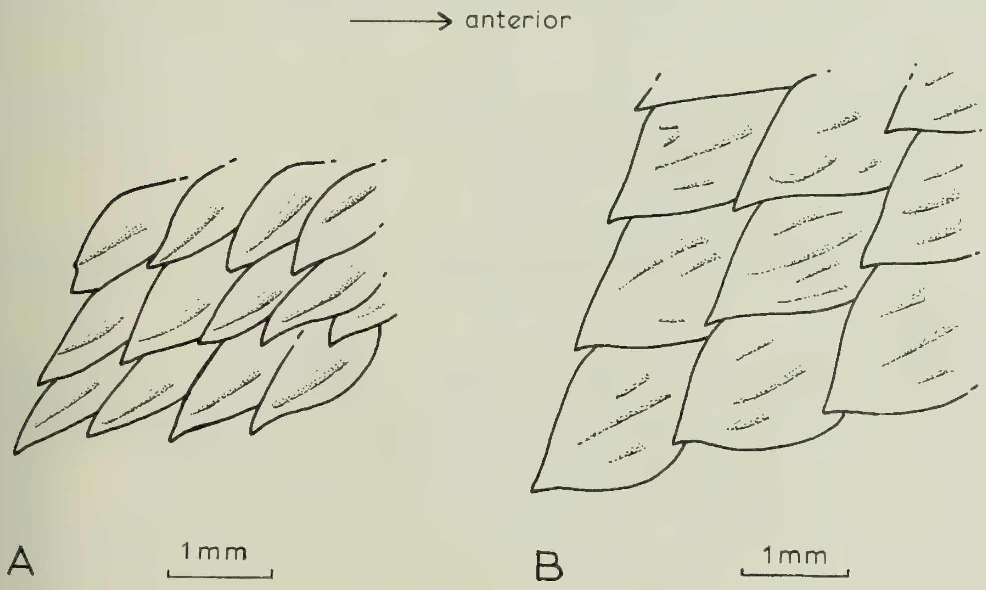

FIG. 14. Anterior flank scales. (A) *Brookvalia gracilis* Wade. P.15827. (B) *Brookvalia latipennis* (Wade). P.15883.

3. Gape wide.
4. Operculum small, quadrangular.
5. Maxilla greatly expanded behind orbit.

There is only one character which is clear in *D. latipennis* and which is not seen in any specimen of *B. gracilis*. In the former species, most scales bear a single, or very occasionally two, rugae orientated obliquely, as is the case in *B. gracilis*. However, in the antero-dorsal region of the body of *D. latipennis* the scales are ornamented with three or four similar rugae—a condition never seen in *B. gracilis* (Fig. 14). There are enough similarities between *D. latipennis* and *Brookvalia* to justify the inclusion of *D. latipennis* in the genus *Brookvalia*, but the presence of the more complex scale ornament in *D. latipennis* warrants separation at the specific level. It is therefore proposed that *Dictyopleurichthys latipennis* be included in the genus *Brookvalia*, but that it should retain its specific name.

Brookvalia spinosa (Wade) comb. nov.

(Fig. 15)

1935 *Beaconia spinosa* Wade: 33–35, text-fig. 17, pl. 6, figs 1–2.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. Extrascapular narrow. Two pairs of parietals; anterior element having long contact with dermopterotic, and bearing a pair of short sensory canals in the shape of an inverted "v". Dermopterotic bearing long posterior extension of the supraorbital sensory canal. No postrostral present. No enlarged teeth at tip of lower jaw.

Body short and relatively deep. Fin rays without bifurcation. Pectoral and pelvic fins equal in size and shape. Dorsal fin as large as the anal fin. Lobes of caudal fin not as deeply cleft as in *B. gracilis*.

Holotype. P.16211.

Material. Holotype and P.16212, U.S.G.D. 14, 33 and 105.

Description. *Size* (Fig. 15). The total length from snout tip to the posterior end of the caudal fin is 46·5 mm (P.16211). The body is fusiform, but relatively deeper than in *B. gracilis*.

Skull and pectoral girdle. The skull is almost identical to that of *B. gracilis*. In particular, two features are seen in the holotype P.16211 which were not described by Wade; these are the presence of an antopercular as well as a dermohyal and the presence of an enlarged branchiostegal ventral to the subopercular. The only differences between the two species are as follows: in *B. spinosa* the extrascapular is oblong and narrow, not broadly pentagonal as in *B. gracilis;* the supraorbital sensory canal runs roughly parallel with the infraorbital sensory canal along almost the entire length of the dermopterotic (the two canals do not meet); and lastly, there are no enlarged teeth at the anterior tip of the lower jaw. The shape of the anterior parietal is slightly different from that of most specimens of *B. gracilis*, but is identical

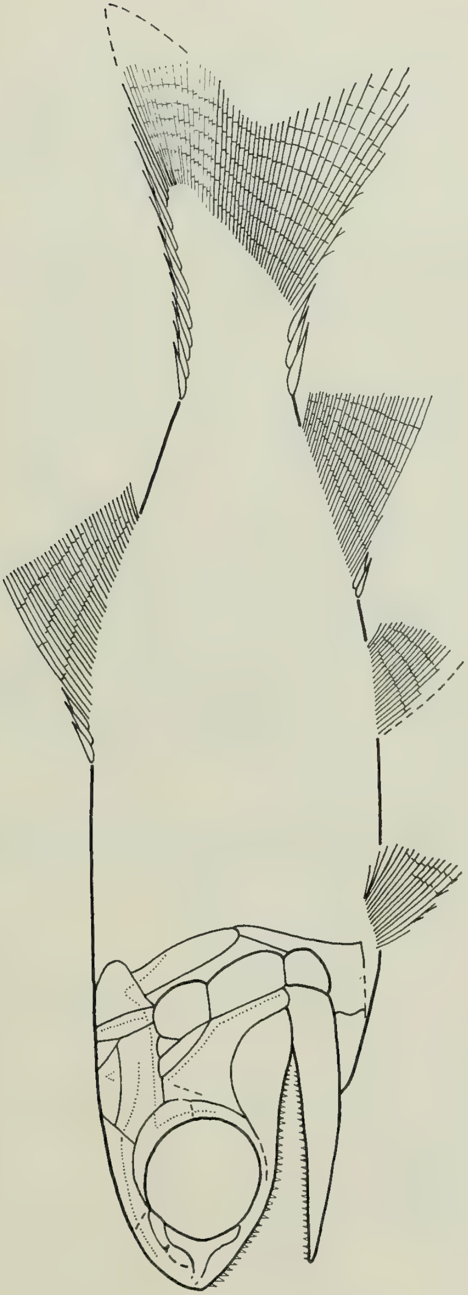

Fig. 15. *Brookvalia spinosa* (Wade). Restoration, ×3·5 approx. Scales omitted.

with that of *B. propennis*. No postrostral is visible; also it is uncertain whether infraorbital elements border the ventral edge of the orbit.

Paired fins. The pectoral fin has 17 rays (U.S.G.D. 105) which have one or two distal joints. A few fringing fulcra are indistinctly visible.

The pelvic fin has 22 rays which have three joints. The anterior margin of the fin is not well enough preserved to show the presence of fringing fulcra. The pelvic fin lies close to the anal fin, there being only three body transverse scale rows between the two. The rays of the paired fins are not bifurcated.

Unpaired fins. None of the unpaired fins has bifurcated rays, nor are there any fringing fulcra preserved on the anal or dorsal fins. The anal fin has 31 rays which have up to 6 equally spaced joints. The dorsal fin has 35 rays which have up to 3 joints.

The distal end of the upper lobe of the caudal fin is not preserved. There are 49 rays, including 29 in the upper lobe of which 8 are epaxial. The longest rays have 10 joints, and a few fringing fulcra are preserved on the anterior edge of the ventral lobe.

Squamation. The exact shape of the scales in fully scaled individuals is difficult to determine. Young individuals, however, are incompletely scaled (U.S.G.D. 14 and 105) and in these the scales are very similar to those seen in young individuals of *B. gracilis*. A single elongate ruga runs across each leaf-shaped scale. In the fully scaled specimen (U.S.G.D. 33) the rugae appear to be paired, but because the outline of the scales is uncertain, it is not possible to be sure whether pairs of rugae occur on single scales, though this is probably the case. There are 40 body transverse scale rows.

DISCUSSION. When first described, *B. spinosa* was assigned to a new genus—*Beaconia*. According to Wade's description (1936 : 33) the diagnostic characters of the genus were the presence of a single X bone, i.e. a dermohyal, but no antopercular, and the absence of a branchiostegal element in the opercular series. All the other features listed in his diagnosis are found also in the genus *Brookvalia*.

It is now clear that an antopercular and a branchiostegal element are in fact present in *B. spinosa*. Moreover, in all other respects the skull of *Beaconia* is almost identical with that of *Brookvalia*. As the diagnostic characters upon which the validity of the genus *Beaconia* depended have been revised, and in view of the general close similarity between *Beaconia spinosa* and *Brookvalia gracilis*, the removal of *Beaconia spinosa* to the genus *Brookvalia* seems to be justified.

At the specific level there are a number of differences between *B. spinosa* and *B. gracilis*. The differences in the construction of the skull are described above. In addition there are several body characteristics which warrant mention: the body is relatively deeper than in *B. gracilis* and the dorsal fin relatively larger and more anterior in position (cf. Figs 8 and 15).

Genus *PHLYCTAENICHTHYS* Wade 1935

1935 *Phlyctaenichthys* Wade: 42.

DIAGNOSIS (emended). Skull bones ornamented with tubercles. Posterior parietal triangular, anterior rectangular, bearing short sensory canals in the shape of an inverted "v". Dermopterotic shallow and elongate, bearing long posterior extension of the supraorbital sensory canal. Frontal curved and elongate, separated from orbit edge by dermosphenotic. Opercular bones wider than in *Brookvalia*, and orientated almost vertically. Preopercular with no contact with dermopterotic. Six suborbital elements. Maxilla separated from the orbit by narrow infraorbitals. Postrostral present. Lower jaw shorter than upper jaw margin.

Body fusiform. Pectoral girdle ornamented with discontinuous, elongate rugae. Scales very deep in lateral line region. Fin rays with many joints. Anal fin small. Dorsal fin with anterior edge lying opposite anterior edge of pelvic fin. Tail hemiheterocercal, deeply bilobate, with high aspect ratio; anterior rays of dorsal lobe bifurcated twice.

TYPE (and only) SPECIES. *Phlyctaenichthys pectinatus* Wade.

DISCUSSION. The outstanding features of this genus are the near vertical suspensorium and the presence of numerous suborbitals. The suborbitals are presumably the product of fragmentation of the single suborbital seen in other redfieldiiforms, and possibly also of the anterior part of the preopercular. These two features are probably related. Gardiner (1967) has shown that with the acquisition of a vertical suspensorium in some palaeoniscoid families (e.g. the Aeduelliidae and the Boreosomidae) the adductor mandibulae probably shifted its origin from the palatoquadrate to the front of the hyomandibular. The pressure of this muscle, together with that of the levator arcus palatini, caused fragmentation of the anterior part of the preopercular and of the suborbitals. A less extreme case is seen in *Perleidus* in which several suborbitals are present, but in which the preopercular is not greatly reduced. The possible explanation of this condition is that the preopercular is prevented from

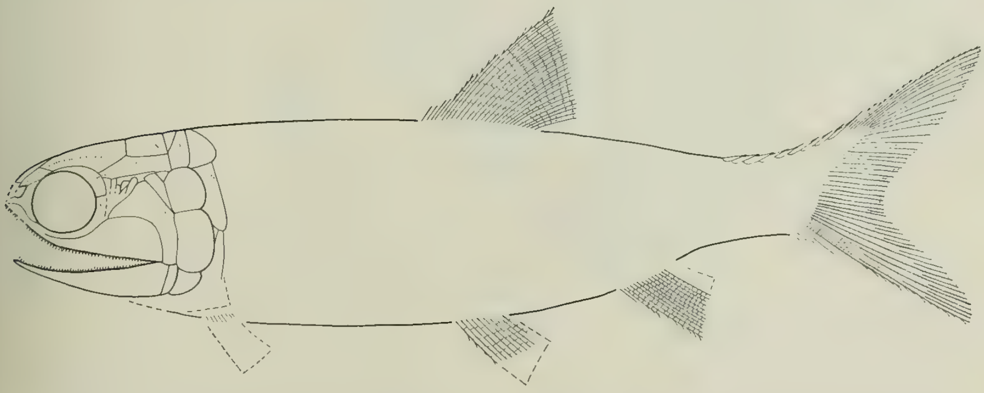

FIG. 16. *Phlyctaenichthys pectinatus* Wade. Restoration, × 1 approx. Scales omitted.

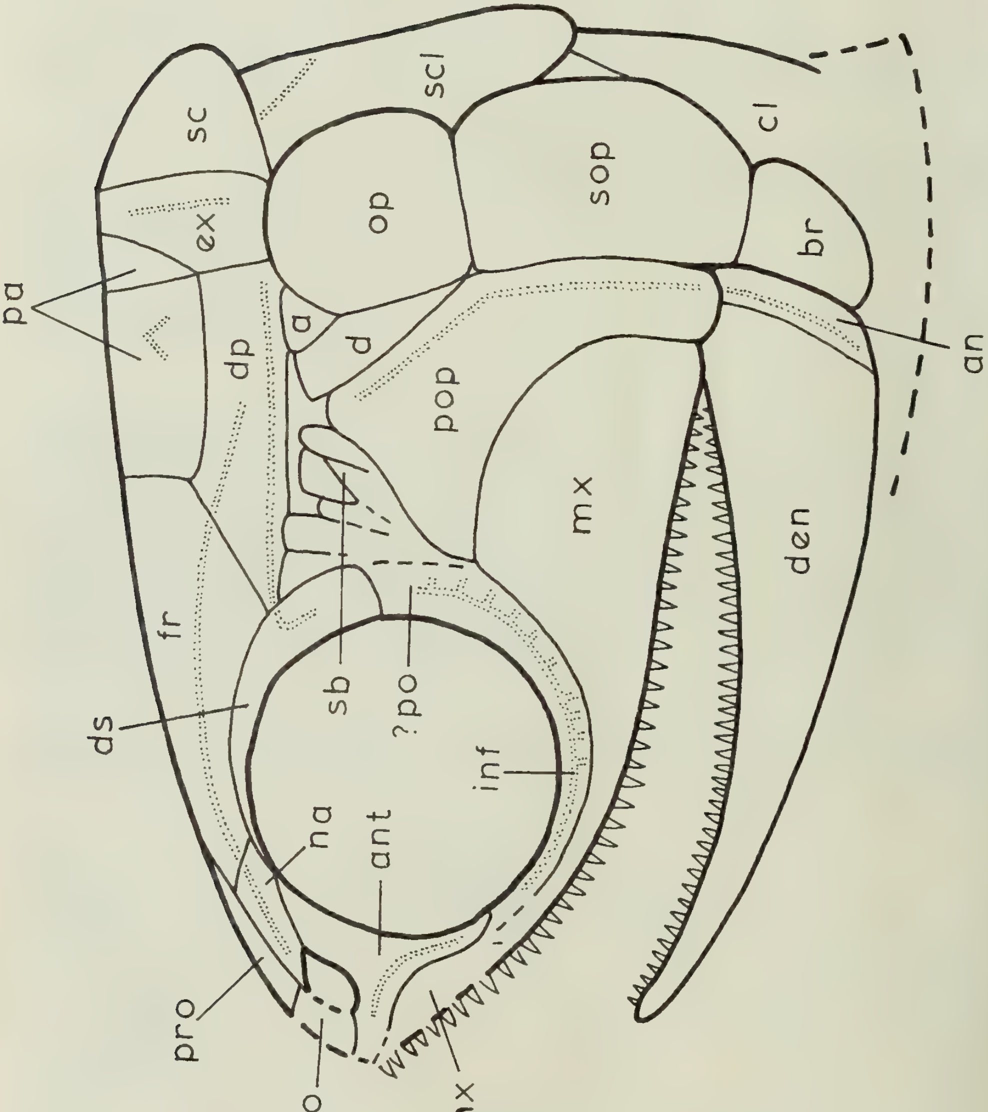
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FIG. 17. *Phlyctaenichthys pectinatus* Wade. Restoration of skull and pectoral girdle. ×7 approx.

more complete fragmentation because part of the adductor mandibulae remains inserted on its interior face. This latter condition is also seen in the Peltopleuriformes, Platysiagiformes and Cephaloxeniformes (Gardiner 1967 : 200). If such a condition does exist in *Phlyctaenichthys*, this genus provides an example of the evolution of such a jaw musculature quite independently within the family Brookvaliidae.

Phlyctaenichthys pectinatus Wade
(Figs 16–18)

1935 *Phlyctaenichthys pectinatus* Wade: 42–44, text-fig. 20, pl. 10, fig. 1.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. As for the genus *Phlyctaenichthys*.

Holotype. U.S.G.D. 200.

Material. Holotype and U.S.G.D. 183, L.12141 and P.16205–6.

Description. *Size.* (Fig. 16). The total length from snout tip to the posterior end of the caudal fin is 137 mm (U.S.G.D. 200). The body is fusiform, its greatest depth occurring between the posterior edge of the head and the level of the dorsal fin.

Skull. (Fig. 17). All the skull bones bear an ornament of numerous small tubercles. Two parietals are present; the posterior element is triangular and overlaps the anterior edge of the extrascapular. The dermopterotic is shallow and elongate, and tapers greatly anteriorly. The infraorbital sensory canal runs close to its ventral edge, and does not join the supraorbital sensory canal.

The opercular series is steeply inclined, the anterior edge of the subopercular lying at 75° to the ventral margin of the maxilla. The opercular is slightly deeper than it is long. The supopercular is 1·3 times as deep and almost exactly the same length as the opercular. An antopercular and a dermohyal lie anterior to the opercular (L.12141, Fig. 18). The outline of the maxilla is more similar to that of North American redfieldiids (Schaeffer 1967) than to other Brookvale forms because the smoothly curved outline of its dorsal border is broken at the point where it meets the antero-ventral corner of the preopercular. The few maxillary teeth which are preserved are 0·75 mm high, pointed and slightly recurved. In specimens P.16206 and L.12141 (Fig. 18), the triangular area below the antero-ventral part of the dermopterotic contains up to six drop-shaped suborbital elements.

A curved dermosphenotic borders the dorsal margin of the orbit, and tapers to a point anteriorly. Sutures between individual infraorbital elements and between the posterior infraorbital and the postorbital are not preserved.

The snout is very similar to that of *Brookvalia*. The antorbital borders the anterior margin of the orbit and has a narrow anterior extension which borders the ventral margin of the nostril, and which carries the ethmoid commissure of the infraorbital sensory canal. Dorsally the antorbital appears to meet the anterior tip of the dermosphenotic, but comparison with other redfieldiiforms suggests that there could be an adnasal in this area. If this is true of *Phlyctaenichthys*, the suture between the antorbital and the adnasal is not preserved.

The snout tip is not preserved, but there was presumably a rostral element which bordered the anterior part of the nostril. Ventral to the anterior extension of the antorbital there is a small knob of bone bearing two teeth (L.12141, Fig. 18); this may be part of the premaxilla which is in evidence further ventrally, and which bears large denticles on its lateral surface, and teeth along its ventral margin. The suture between the premaxilla and the maxilla is not preserved, but its position is indicated by a change in surface ornament from denticles (premaxilla) to smaller tubercles (maxilla).

Lower jaw. The lower jaw tapers anteriorly and its end is upturned. Fifteen teeth only are preserved which are almost 0.75 mm high (P.16205). They appear to be blunt, but this may be due to poor preservation. The tip of the lower jaw does not extend as far as the tip of the snout.

Pectoral girdle. The supracleithrum extends ventrally to a point almost midway down the posterior edge of the subopercular, and bears an ornament of sinuous ridges, which are broken to form discrete rugae on its postero-dorsal part. Except for the dorsal part of the cleithrum, which is narrow, the rest of pectoral girdle is not preserved.

Paired fins. Nothing is known of the pectoral fin except that it has 8 rays. The

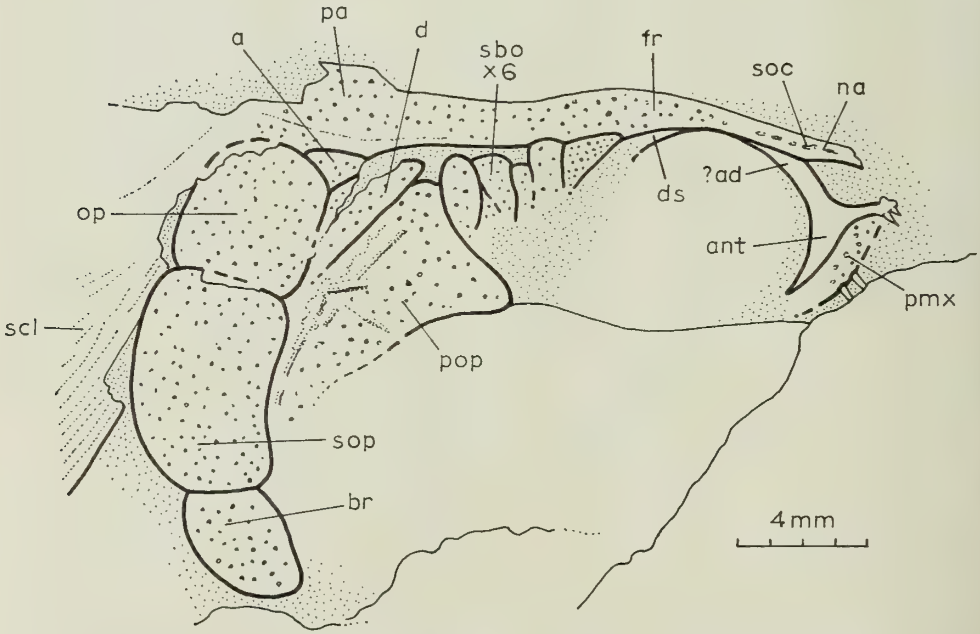

FIG. 18. *Phlyctaenichthys pectinatus* Wade. L.12141: impression of left side.

pelvic fin is also incompletely preserved. It has at least 10 rays which have 5 joints. The anterior ray bears fringing fulcra. There is no distal bifurcation.

Unpaired fins. The anal fin is small and has at least 15 rays which have up to 15 joints. The joints are closely spaced and equal the number of fulcra on the distal parts of the anterior rays. There is no distal bifurcation. The dorsal fin has 25 rays which have up to 12 joints. The anterior rays bear fringing fulcra, and the central rays bifurcate along half their length. The caudal fin is deeply cleft and has a high aspect ratio. There are 43 rays, 27 in the dorsal lobe, and the longest rays have at least 50 joints. The anterior rays on both lobes of the tail bear fringing fulcra. In the dorsal lobe the first 9 rays are epaxial in position. All the caudal fin-rays bifurcate; in addition, the anterior rays of the dorsal lobe bifurcate a second time at their distal ends.

Squamation. The body scales, except for those in the lateral line region, are leaf-shaped, but overlap to give a rhomboidal pattern. The largest flank scales are 1·6 mm long and 4 mm deep (U.S.G.D. 183) but nearer the dorsal and ventral edges of the body the scales are equidimensional. There are 40 body transverse scale rows.

Family **REDFIELDIIDAE** Berg 1940

Diagnosis. Orbit small. One pair of parietals usually present, but sometimes three or four (one pair + one, or two pairs) present. Dermosphenotic equal in size to dermopterotic. Posterior extension of supraorbital sensory canal, if present, on parietal. Dermosphenotic rectangular, widely separating frontal from dorsal orbital edge. Snout composed of rostral and paired antorbitals and nasals. Snout elements ornamented with large tubercles, presumably specialized for support of fleshy lip. Postrostral usually present, but reduced or lost in some Upper Triassic genera. Antorbital broad, bordering anterior edge of orbit; posterior, ventral, and sometimes anterior, edges of nostril; and ventral edge of snout. No premaxilla. Large adnasal with broad contact with antorbital and dermosphenotic. A single dermohyal present. No antopercular, except in two species of one genus (*Helichthys*). Maxilla narrow anteriorly and separated from orbital edge by complete infraorbital series. Gular plate present. Lower jaw deep, short and either straight or curved dorsally towards the symphysis.

Elements of pectoral girdle generally broad. Fulcra usually well developed on all fins. Scales rhomboidal to leaf-shaped, often with denticulated posterior borders. Hinge line at base of body lobe of tail not marked by abrupt change in orientation of scale rows.

Genus ***DAEDALICHTHYS*** Brough 1931

1931 *Daedalichthys* Brough: 245.

Diagnosis (emended). Head bullet-shaped with snout extended to form a pronounced rostrum. Skull bones ornamented with large tubercles and with posterior margins frequently denticulated. A single pair of parietals. Dermopterotic rhombic. Frontal rectangular and elongate, separated from the orbit edge by a deep dermosphenotic. Adnasal almost square with broad contact with dermosphenotic. Nasals elongate. Rostral bordering the anterior edge of the nostril, and forming an overhanging rostrum at snout tip. Postrostral present. Opercular series moderately oblique. A single suborbital present. Maxilla deep posteriorly, antero-dorsal edge overlapped by broad infraorbital elements. Teeth pointed and slightly recurved. Lower jaw stout and straight.

Posterior margins of suprascapular and supracleithrum denticulate. Scales rhombic, ornamented with ridges, and with denticulated posterior borders. Fin-rays with large fulcra. Paired fin-rays stout, unjointed and few in number. Unpaired fin-rays numerous, delicate and with regular jointing. Caudal fin hemi-heterocercal.

TYPE (and only) SPECIES. *Daedalichthys higginsi* Brough.

REMARKS. Apart from the presence of two branchiostegals, *Daedalichthys* is remarkable for its similarities with North American redfieldiids of the Upper Triassic (Schaeffer 1967). The characteristic arrangement of the bones of the snout and cheek appears to have changed very little during the Triassic, and enables the family Redfieldiidae to be easily recognized and defined.

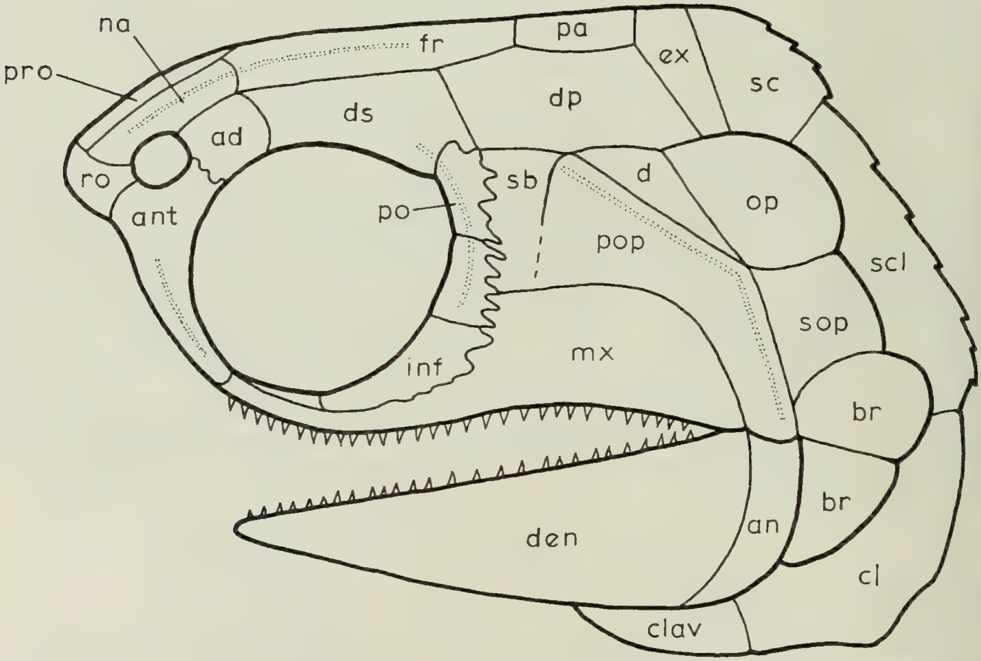

FIG. 19. *Daedalichthys higginsi* Brough. Restoration of skull and pectoral girdle, ×5·5 approx.

Daedalichthys higginsi Brough
(Figs 19–20)

1931 *Daedalichthys higginsi* Brough: 245–246, text-fig. 3, pl. 1. fig. 4.
1934 *Daedalichthys higginsi* Brough; Brough: 559–564, text-fig. 1, pl. 1, fig. 1.

Horizon and locality. Scythian. Lower Cynogathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis. As for the genus *Daedalichthys*.

Holotype. G.N. 301.

Material. Holotype, P.17532–3 and P.17538.

Description. Study of specimens G.N. 301 and P.17532–3 enables some additions and some corrections to be made to the otherwise complete description of *D. higginsi* (Brough 1934).

The area occupied by the nasal in Brough's figure (1934 : text-fig. 1) in fact contains two elements, the adnasal and antorbital. The antorbital forms the anterior border of the orbit as it does in other redfieldiiforms; its identification is confirmed by the presence of pits leading into the infraorbital sensory canal. In specimen G.N. 301 (Fig. 20) the ventral parts of both antorbitals are damaged, revealing tubes along which the sensory canal itself ran. The adnasal is also clearly seen in specimen G.N. 301.

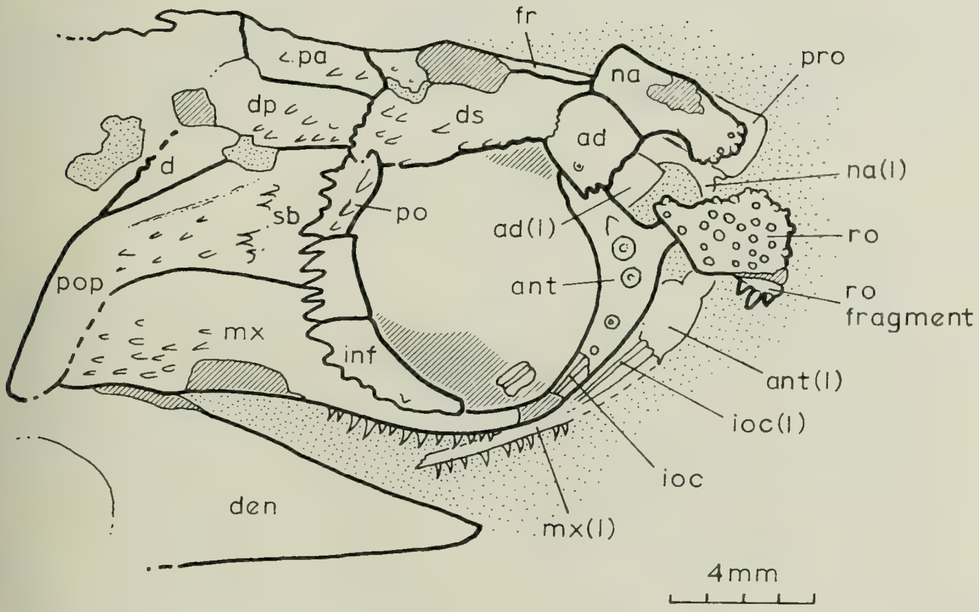

Fig. 20. *Daedalichthys higginsi* Brough. G.N. 301: right side unless otherwise indicated.

Identification of the antorbital and adnasal in *D. higginsi* necessitates reinterpretation of the other snout elements, and makes a new restoration of the whole skull possible (Fig. 19). A curved nasal (second postrostral of Brough) lies anterior to the frontal. It forms the dorsal border of the nostril. Between the nasals there is a postrostral which extends posteriorly between the anterior ends of the frontals. The snout tip is formed by an ornamented rostral which gives the snout its singular profile. In specimen G.N. 301 (Fig. 20) there is a fragment of bone lying ventral to the main part of the rostral, and separated from it by an area of crushed bone. At first this appeared to be a premaxilla, mainly because teeth seemed to be present on its ventral border. Closer inspection, however, shows that these tooth-like projections are identical with the tubercles found on other parts of the snout, and differ from the maxillary and dentary teeth in that they are neither as pointed, nor are they slightly recurved. It is therefore concluded that this fragment represents the ventral part of the rostral, and that there is no premaxilla in *Daedalichthys*.

The only other additions to Brough's description of *D. higginsi* are the identification of a single wedge-shaped dermohyal lying anterior to the opercular, and a suture between the angular and dentary. Modifications of Brough's restoration are seen in a slight change in the angle of the suture which subdivides the branchiostegal (a variable feature in the genus), and in the identification of only a single suborbital (second postorbital of Brough). Brough (1934 : 563) has already noted that there is some variation in the sutural pattern between elements of the opercular series. There was no sign, in the specimens studied, of subdivision of the extrascapular (tabular of Brough), a condition suggested by Brough (1934 : 560).

With the exception of one point, the identification of fringing fulcra on the rays forming the anterior edge of the ventral caudal lobe, no additions can be made to Brough's description of the postcranial anatomy of *Daedalichthys*.

Genus ***HELICHTHYS*** Broom 1909

1909 *Helichthys* Broom: 254.
1931 *Helichthys* Broom; Brough: 246.

The genus *Helichthys* was erected by Broom (1909) to accommodate three species; *H. browni*, *H. draperi* and *H. tenuis*. In 1931 Brough revised the genus and removed the species *H. draperi* and *H. tenuis* to the palaeoniscoid genus *Dicellopygae*, but retained *H. browni* as the type species. In addition, the following new species from the Bekker's Kraal fauna (Lower Cynognathus zone), Orange Free State, were added to the genus: *H. elegans*, *H. stegopygae*, *H. obesus*, *H. ctenipteryx* and *H. grandipennis*.

The validity of Brough's species is not contested here, but one of them, *H. elegans*, has been restudied and a new restoration of the dorsal bones of the snout given.

Diagnosis (emended). Head blunt, with small orbit. Skull bones usually ornamented with ridges and tubercles but may be nearly smooth. Two pairs of parietals similar in shape to those of *Brookvalia*, both bearing short paired sensory canals. Dermopterotic roughly rectangular, but narrow posteriorly. Frontal elongate. Adnasal deep with broad contact with dermosphenotic. Nasal short.

Rostral bordering anterior edge of nostril. Postrostral present. Opercular series moderately oblique. Subopercular and branchiostegal divided by a straight suture. Antopercular may or may not be present. A single suborbital present. Teeth conical and sharply pointed. Lower jaw stout and straight.

Body fusiform. Pectoral girdle large and ornamented with strong ridges. Scales rhombic to leaf-shaped, unornamented. Fin-rays with large fulcra. Pectoral fin-rays stout, jointed distally or not at all, other fin-rays with regular jointing. Caudal fin hemiheterocercal and equilobate.

TYPE SPECIES. *Helichthys browni* Broom.

Helichthys elegans Brough
(Figs 21–22)

1931 *Helichthys elegans* Brough: 248–252, text-figs 4–5, pl. 2, figs 1–2.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS. As in Brough (1931 : 248). Only one alteration need be made to

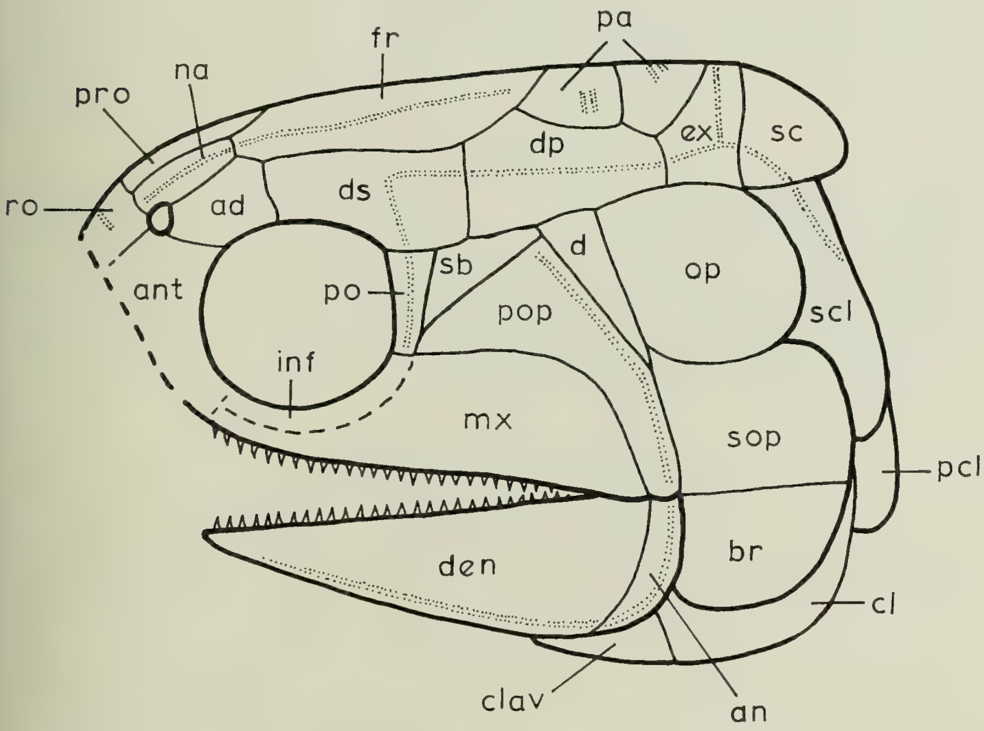

FIG. 21. *Helichthys elegans* Brough. Restoration of skull and pectoral girdle, ×6 approx.

Brough's diagnosis; restoration of the snout region shows that the orbit can no longer be regarded as having '. . . an extreme anterior position in the head'.

HOLOTYPE. A specimen in the D. M. S. Watson collection (missing from the Cambridge University Zoology Department collection).

MATERIAL. G.N. 316.

DESCRIPTION. Brough did not describe the snout region in any species of *Helichthys*. In an attempt to remedy this omission, Schaeffer has made a new restoration of the skull of *Helichthys* based upon material in the A.M.N.H. (1967 : text-fig. 17B). This restoration is slightly inaccurate however, mainly because the adnasal is figured without contact with the nostril border. An almost perfectly preserved skull roof of *H. elegans* from the Cambridge University Zoology Department collection (G.N. 316, fig. 22) makes an accurate restoration of most of the snout of *Helichthys* possible (Fig. 21). Specimen G.N. 316 shows that the dorsal

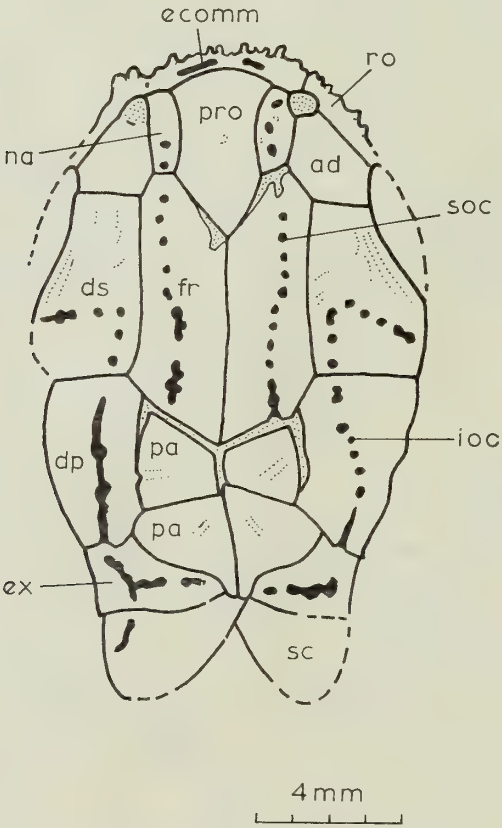

FIG. 22. *Helichthys elegans* Brough. G.N. 316: dorsal view.

part of the snout in *Helichthys* is almost identical to that of *Cionichthys* and *Redfieldius* (Schaeffer 1967). The difference between *Cionichthys* and *Redfieldius* is that in the latter genus the adnasal extends considerably further posteriorly than does the nasal, whereas in *Cionichthys* these two bones extend posteriorly to the same level. *Helichthys* shows an intermediate condition in that the adnasal extends only slightly further posteriorly than does the nasal.

The only other major difference between Brough's figures of *Helichthys* and the restoration given here is that the sensory canal on the preopercular is not joined to the infraorbital sensory canal on the dermopterotic.

Genus ***GEITONICHTHYS*** Wade 1935

1935 *Geitonichthys* Wade: 37.

Diagnosis (emended). Skull deep, orbit small. Dermopterotic deep and oblong. Frontal not as elongate as in *Molybdichthys*. Dermosphenotic deep, with ornament of ridges on its ventral edge. Antorbital wide, bordering the whole of the ventral border of the nostril. Opercular deeper than long. Opercular series narrow, inclined steeply. Preopercular with short contact with dermopterotic. A single narrow triangular suborbital, and a narrow rectangular postorbital present.

Elements of pectoral girdle broad. All fin-rays jointed. Dorsal and anal fins opposite one another and posterior in position. Bifurcation visible only in caudal fin-rays.

Type (and only) species. *Geitonichthys ornatus* Wade.

Remarks. *Geitonichthys*, together with *Molybdichthys*, has been placed in the Redfieldiidae. However, these genera are not typical of the family, and details such as the shape of the antorbital and of the lower jaw separate the Australian genera from the redfieldiids of Africa and America. There is not enough evidence to justify the erection of a separate family for *Geitonichthys* and *Molybdichthys*, but it should be noted that these genera probably represent redfieldiid populations which were, in some way, isolated from the 'mainstream' of redfieldiid evolution.

Geitonichthys ornatus Wade
(Figs 23–24)

1935 *Geitonichthys ornatus* Wade: 37–39, text-fig. 18, pl. 8, fig. 2.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. As for the genus *Geitonichthys*.

Holotype. P.15859.

Material. Holotype and P.15880.

Description. *Size.* The total length of the holotype (the larger of the two specimens) is estimated to be 120 mm. The body is fusiform, its greatest depth occurring midway between the posterior edge of the operculum and the anterior edge of the dorsal fin.

Skull (Fig. 23). The postero-dorsal part of the skull and parts of the snout tip are missing in both specimens. The frontal is deep and rectangular. The large dermosphenotic bears four ridges ventrally which follow the outline of the dorsal margin of the orbit. The dorsal edge of the dermosphenotic is clear but, below this, the bone surface is eroded and the anterior extension of the infraorbital sensory canal figured by Wade (1935 : text-fig. 18) cannot be seen. In specimen P.15880 (Fig. 24) the dermosphenotic is displaced ventrally, relative to the adnasal, by about 1 mm; its probable position has been restored in Fig. 23. The dermopterotic is also extensive and is roughly rectangular. The suprascapular and extrascapular are either missing (P.15880) or poorly preserved (P.15859) and, although their outlines cannot be traced, numerous elongate tubercles are seen where they occur.

The anterior edge of the subopercular lies at 68° to the ventral margin of the maxilla. A single triangular branchiostegal ray is present, fitting closely to the posterior edge of the lower jaw. A single wedge-shaped dermohyal lies anterior to the opercular. The preopercular is 'r'-shaped and has point contact with the dermopterotic. There is a single triangular suborbital.

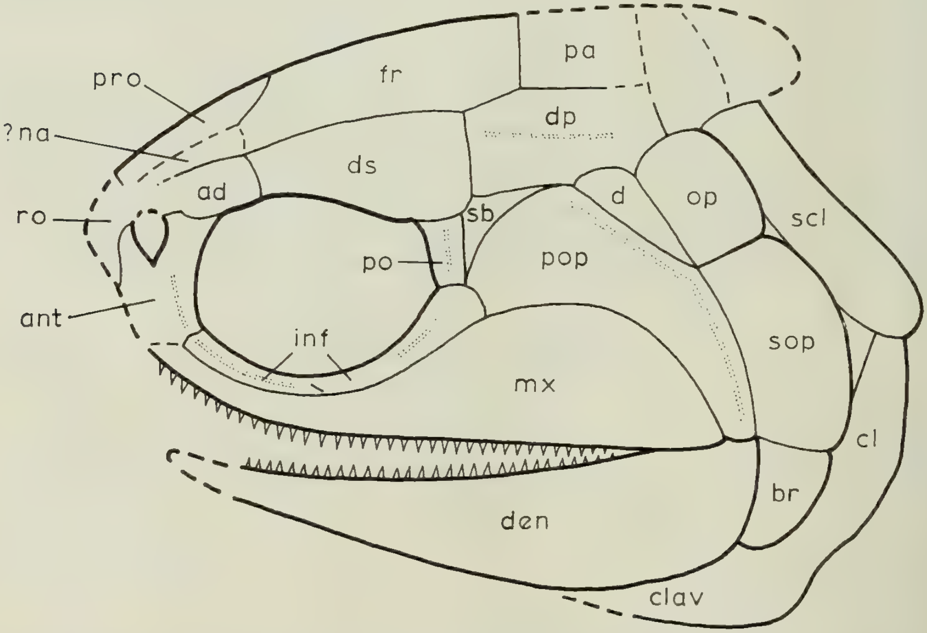

FIG. 23. *Geitonichthys ornatus* Wade. Restoration of skull and pectoral girdle, ×5 approx.

Few teeth are preserved, but those present are pointed and 0·5 mm high (P.15859). In specimen P.15880 (Fig. 24) numerous palatine teeth 0·1 mm in diameter are visible in cross section near the ventral edge of the maxilla.

A curved bone lies anterior to the frontal. Its anterior extent is seen in P.15859 where it is disarticulated from whatever element lay further anteriorly. It bears a ridge which runs antero-ventrally towards the nostril (P.15880, Fig. 24), but whether this is associated with a sensory canal is not clear. The most likely interpretation of this region is that this is a postrostal and that it has been displaced ventrally, thus obscuring a narrow nasal. Anterior to the dermosphenotic, and bordering the orbit between the dermosphenotic and the antorbital, is an adnasal. Its anterior extent is not known. Its ventral margin bears a low ridge which follows the outline of the bone and curves dorsally for a short distance between the orbit and the nostril. If the anterior edge of the adnasal follows this ridge dorsally, the adnasal does not reach the nostril border. This restoration would imply that the nasal ran behind the nostril to meet the dorsal edge of the antorbital. An alternative restoration can be made in which the adnasal extends antero-ventrally to the posterior edge of the nostril. Comparison with *Molybdichthys* and Upper Triassic redfieldiids from N. America suggests that the latter interpretation is more likely to be correct.

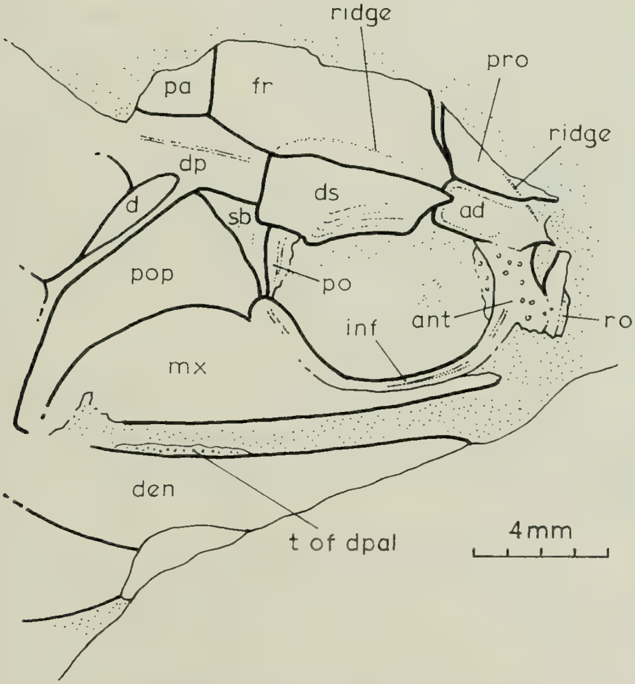

FIG. 24. *Geitonichthys ornatus* Wade. P.15880: right side.

The nostril is an inverted drop shape. The antorbital is wide and bears numerous tooth-like denticles. The snout tip is missing and in consequence the exact anterior extent of the maxilla is not known; also it is not known if a premaxilla was present. There is a ridge running from the anterior edge of the nostril ventrally, and this may mark the anterior end of the antorbital, but there is no suture visible. There was presumably a rostral on the snout tip, and its presence is suggested by a few traces of tubercles in that area (Fig. 24), but its extent, and thus the profile of the snout, is unknown.

Lower jaw. The dentary bears an ornament of fine elongate ridges. Teeth on the lower jaw are not clearly preserved.

Sensory canal system. The infraorbital sensory canal is clearly seen on the dermopterotic (P.15880, Fig. 24) but its anterior extension on the dermosphenotic, figured by Wade (1935 : text-fig. 18), cannot be traced. As mentioned above, in specimen P.15880 the dermosphenotic has been displaced ventrally, but the probable original position of its dorsal edge is represented by a shallow ridge running along the ventral edge of the frontal. In Wade's figure this ridge has been misinterpreted as a sensory canal. There are no clear traces of the supraorbital sensory canal.

Pectoral girdle. The bones of the pectoral girdle all bear an ornament of well defined, elongate rugae. The supracleithrum extends to a point more than midway along the posterior edge of the subopercular. No postcleithrum is visible.

Paired fins. The pectoral and pelvic fins in both specimens of *G. ornatus* are either missing or so poorly preserved that no useful observations can be made regarding their structure.

Unpaired fins. Only a fragment of the anal fin is preserved in specimen P.15859. There are at least 15 jointed rays.

The dorsal fin is triangular and has 22 rays, each with 7 or 8 joints. The anterior rays bear fringing fulcra, and no distal bifurcation was observed.

The caudal fin is preserved with part of the dorsal lobe missing. There are at least 40 rays with up to 17 joints. The tips of some rays in the ventral lobe are bifurcated, and the anterior rays bear fringing fulcra.

Squamation. The scales are leaf-shaped. Those near the dorsal and ventral edges of the body are relatively more elongate than those in the lateral line region. The largest flank scales are 1·5 mm long and just over 1 mm deep (P.15859). There are about 50 body transverse scale rows, containing 22 scales in the pectoral region, and 19 in the dorsal fin region. The scales lack ornament, but this may be due to poor preservation.

Genus ***MOLYBDICHTHYS*** Wade 1935

1935 *Molybdichthys* Wade: 39.

DIAGNOSIS (emended). Skull deep, orbit fairly small. One pair of parietals, roughly square, and bearing a pair of sensory canals in the shape of an inverted 'v'. Dermopterotic moderately deep anteriorly, narrower posteriorly. Frontal long and deep. Dermosphenotic deep, with ornament of ridges on its ventral edge. Nasal narrow and rectangular. Antorbital wide, bordering the postero-ventral edge of the nostril. Opercular longer than deep. Opercular series broad, orientated almost vertically. Preopercular with short contact with the dermopterotic. Maxilla deeper than in *Geitonichthys* posteriorly. Single large suborbital. Postorbital region wide.

Elements of pectoral girdle extremely broad. Fin-rays bifurcated and with many joints. Dorsal and anal fins opposite one another and posterior in position.

TYPE (and only) SPECIES. *Molybdichthys junior* Wade.

REMARKS. *Molybdichthys* is very similar to *Geitonichthys*, and differences can be related mainly to the presence of a more upright suspensorium.

Molybdichthys junior Wade

(Figs 25–27)

1935 *Molybdichthys junior* Wade: 40–42, text-fig. 19, pl. 7, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Molybdichthys*.

HOLOTYPE. P.16204.

MATERIAL. Holotype and P.16207–8, P.16822, P.24695–6, U.S.G.D. 43, 146, 216.

DESCRIPTION. *Size.* (Fig. 25). Specimen P.16822 is almost complete; its length from snout tip to the posterior end of the caudal fin is about 145 mm. The maximum body depth occurs between the paired fins.

Skull. (Fig. 26). In most respects the skull of *Molybdichthys* resembles that of *Geitonichthys* and it has been found convenient to compare the two in the following description.

The frontal and dermosphenotic are similar in shape in both genera; also, in both the dermosphenotic bears an ornament of ridges along the dorsal border of the orbit. In *Molybdichthys* the parietal bears a pair of sensory canals in the shape of an inverted 'v'.

In *Molybdichthys* the opercular is relatively shorter, and all three elements of the opercular series are considerably wider than in *Geitonichthys*. The opercular series is nearer vertical; the anterior edge of the subopercular lies at 80° to the level of the ventral edge of the maxilla. The preopercular is overlapped anteriorly by a large triangular suborbital. The preopercular has very short contact with the dermopterotic. A single wedge-shaped dermohyal is present.

The maxilla is similar in shape to that of *Geitonichthys*, but is slightly deeper posteriorly. A few maxillary teeth are preserved, and about 50 are calculated to have been present.

The posterior edge of the orbit is bordered by a postorbital element which is somewhat wider than that of *Geitonichthys*. The anterior edge of the orbit is bordered

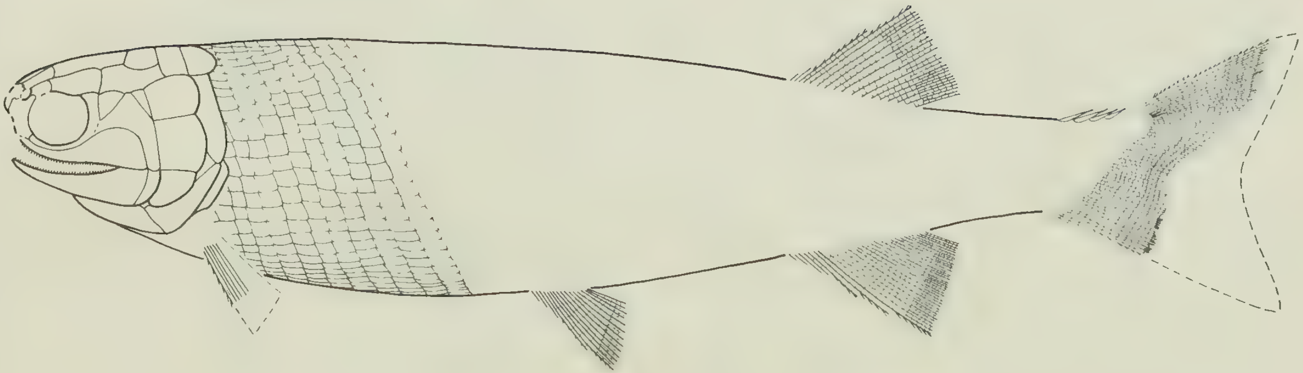

FIG. 25. *Molybdichthys junior* Wade. Restoration, × 1 approx. Posterior scales omitted.

by an antorbital which bears tooth-like denticles. Its ventral edge is not completely clear so that it is not possible to determine the exact relationship between the antorbital and the maxilla. The antero-dorsal edge of the antorbital borders part of the posterior edge of the nostril. Dorsal to the antorbital there are traces of an adnasal which also borders the nostril, and probably part of the orbit.

The rest of the snout has been restored from the crushed remains of specimens P.16822 and U.S.G.D. 43. In P.16822 (Fig. 27) there is a large postrostral which caps the snout. Lateral to this is a rectangular nasal which bears the anterior extension of the supraorbital sensory canal (only the right nasal is preserved in P.16822). The postrostral has been crushed ventrally onto the rest of the snout. The snout tip is completed by a rostral which is incompletely preserved; it bears tooth-like denticles.

Lower jaw. The dentary is deep posteriorly and tapers anteriorly. Some variation in the maximum depth of the dentary was observed in several specimens of *M. junior* but as no other details of the skull could be observed in these, it could not be definitely established whether this variation represented distinction at the specific

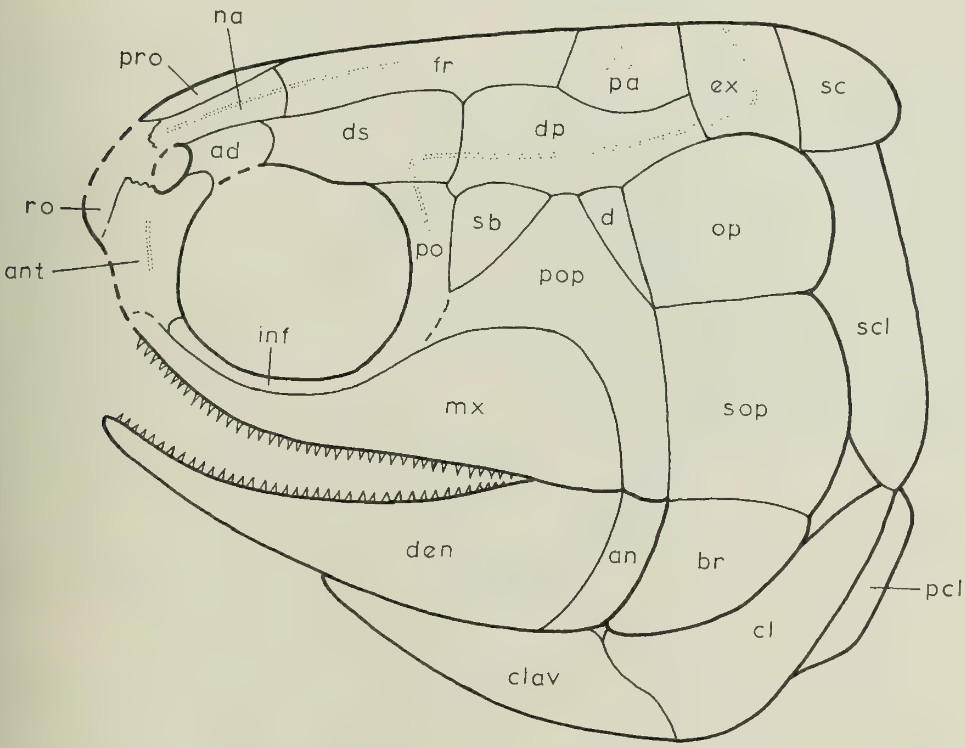

FIG. 26. *Molybdichthys junior* Wade. Restoration of skull and pectoral girdle, ×4·5 approx.

level. Provisionally therefore, all the known specimens are retained in a single species.

The dentary bears an ornament of elongate ridges. About 50 conical teeth are calculated to have been present.

Pectoral girdle. The supracleithrum extends to a point two-thirds of the way along the posterior edge of the subopercular. It bears an ornament of parallel ridges, as does the cleithrum. The cleithrum and clavicle are broad and the latter extends at least halfway along the ventral edge of the lower jaw. An elongate, ornamented postcleithrum is present.

Paired fins. A fragment of the pectoral fin is preserved in specimen U.S.G.D. 216. Little can be determined except that at least 6 rays are present. They appear to be unjointed, fringing fulcra are present and there is distal bifurcation of at least one ray.

The pelvic fin has at least 14 stout rays, with 6–7 joints. The anterior rays bear fringing fulcra and there is distal bifurcation.

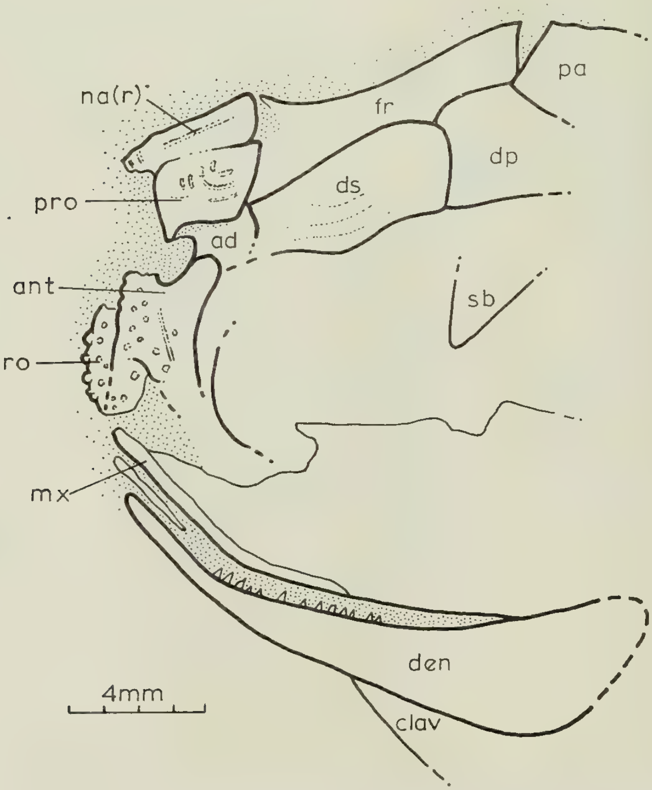

FIG. 27. *Molybdichthys junior* Wade. P.16822: left side unless otherwise indicated.

Unpaired fins. All the unpaired fin-rays bifurcate distally and the leading rays have fringing fulcra. The anal fin has 30 rays, the longest of which have 20 joints.

The dorsal fin lies just anterior to the level of the anal fin. There are 17 rays which have up to 15 joints.

The distal part of the ventral lobe of the caudal fin is missing. There are 26 rays in both the dorsal and ventral lobes, with at least 19 joints. In the dorsal lobe the rays bifurcate first at the 13th joint and again at about the 19th joint.

Squamation. The scales are very variable in shape. Anteriorly they are rhomboidal, up to 2·8 mm long and 3·5 mm deep in the lateral line region; towards the dorsal and ventral margins the scales are less than 1 mm deep while remaining up to 2 mm long. Posteriorly the scales are leaf-shaped and are 2 mm long and 1·5 mm deep. No ornament is preserved. There are 44 body transverse scale rows which contain up to 20 scales.

Family **SCHIZURICHTHYIDAE** nov.

DIAGNOSIS. As for the genus *Schizurichthys*.

Genus ***SCHIZURICHTHYS*** Wade 1935

1935 *Schizurichthys* Wade: 44.

DIAGNOSIS (emended). Skull incompletely known. Head wedge-shaped. Dermosphenotic narrow and crescent-shaped, tapering anteriorly. Antorbital expanded ventrally below the nostril, but separated from the ventral edge of the snout by a narrow toothed element. No postrostral. Opercular elements 'D'-shaped, ornamented with radiating rows of tubercles. Opercular and subopercular inclined steeply. An antopercular and a dermohyal present. Lower jaw as long as the upper jaw, curved dorsally towards the symphysis.

Body moderately deep. Scales equidimensional to rectangular, with ornament of radiating rows of tubercles, and with a dorsal peg and a ventral notch. All fins with fringing fulcra and (with the possible exception of the pectoral) with bifurcated rays. Rays of pectoral fin unjointed, of pelvic fin partly jointed. Rays of unpaired fins jointed many times. Caudal fin hemiheterocercal, with epaxial lobe of six rays of which the first and sixth bear fringing fulcra.

TYPE (and only) SPECIES. *Schizurichthys pulcher* Wade.

REMARKS. The genus *Schizurichthys* was previously included in the Catopteridae (Redfieldiidae).

Schizurichthys pulcher Wade
(Figs 28–30)

1935 *Schizurichthys pulcher* Wade: 44–46, text-fig. 21, pl. 10, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS. As for the genus *Schizurichthys*.

HOLOTYPE. P.15892.

MATERIAL. Holotype, P.15891 and U.S.G.D. 305.

DESCRIPTION. *Size.* (Fig. 28). The best preserved specimen of *S. pulcher* is U.S.G.D. 305. Its total length from snout tip to the posterior end of the caudal fin is about 235 mm. The body is fairly deep, its greatest depth occurring between the paired fins.

Skull. (Fig. 28). In lateral view the skull is wedge-shaped, tapering anteriorly to a blunt snout. The outlines of the dorsal bones immediately anterior to the suprascapular cannot be distinguished. A narrow frontal is incompletely preserved.

The opercular and subopercular bones are 'D'-shaped. A single branchiostegal is present (P.15891) and has similar dimensions to the opercular. The opercular series is moderately oblique; the anterior margin of the subopercular lies at 65° to the ventral margin of the maxilla. All the opercular bones are ornamented with lines of rugae which radiate from a point close to the antero-dorsal corner of each element. The presence of antopercular and dermohyal elements is inferred from two indentations in the ventral margin of the dermopterotic. The cheek region is poorly preserved. The maxilla is similar in shape to that of *B. gracilis*, but its narrow anterior portion is badly crushed, and it cannot be determined whether it borders the ventral margin of the orbit or if it is separated from the latter by infraorbital elements. The maxilla bears about 50 conical teeth, which are up to 1·5 mm high.

The postero-dorsal edge of the orbit is bordered by a curved dermosphenotic which appears to taper to a point anteriorly (U.S.G.D. 305, Fig. 29). Its posterior edge is not preserved. The antero-dorsal edge of the orbit appears to be bordered by a narrow diamond-shaped adnasal, but this too, is poorly preserved. The nostril, visible as a notch in the antorbital, is large; dorsally it is bordered by a narrow nasal which bears traces of part of the supraorbital sensory canal (U.S.G.D. 305, Fig. 29). Ventral to the nostril the antorbital is deep, and further ventrally a tooth-bearing element extends to the snout tip, but it cannot be determined whether this is a premaxilla or the anterior part of the maxilla.

Pectoral girdle. The supracleithrum extends ventrally to a point halfway down the posterior edge of the subopercular. The dorsal part of the cleithrum is slender and lanceolate. Both bones are ornamented with numerous ridges which run parallel to the edges of the bones. The suture between the cleithrum and clavicle is not visible.

Paired fins. The pectoral fin has at least 12 stout rays (P.15891). Joints are not visible and distal bifurcation is not preserved. The anterior ray bears numerous fringing fulcra. The pelvic fin has 25 stout rays which bifurcate about midway along their length. Up to 3 joints are visible on the proximal parts of the anterior rays. Fringing fulcra are borne by the anterior rays.

Unpaired fins. All the rays of the unpaired fins are bifurcated, and all bear tiny tubercles on their proximal parts. The anal fin is large. There are at least 41 stout

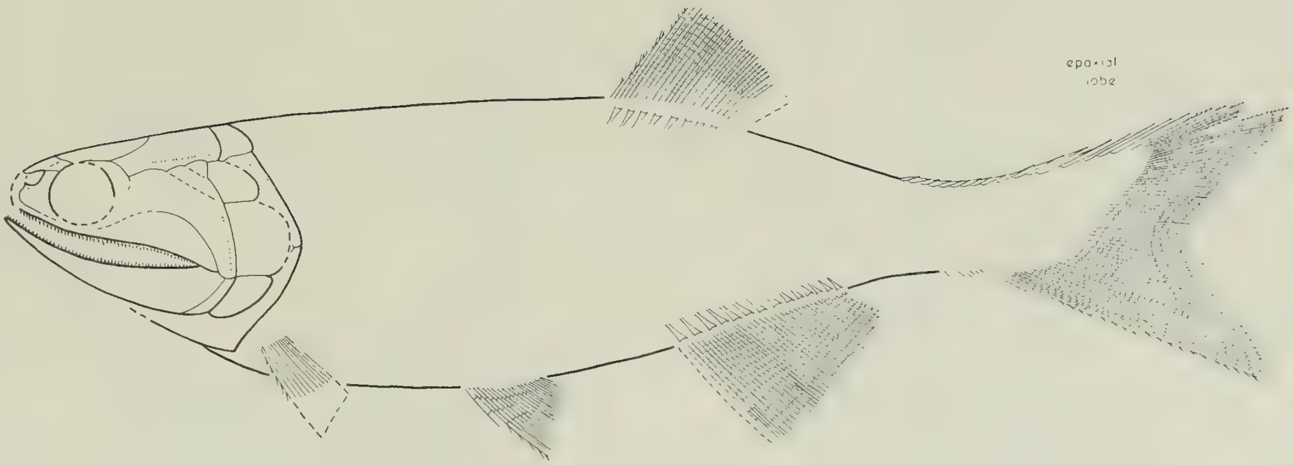
epaxial
lobe

FIG. 28. *Schizurichthys pulcher* Wade. Restoration, ×0·75 approx.

rays with up to 14 joints. The anterior rays are not preserved. The anal fin is supported by at least 14 radials (each therefore associated with three rays) which have wide, spatulate distal ends.

The dorsal fin is slightly smaller than the anal fin, but is similar in shape. There are at least 22 rays, which have up to 20 joints, and those along the anterior edge bear fringing fulcra.

The caudal fin is equilobate. There are 34 rays in the dorsal lobe and 35 in the ventral lobe. All the rays bifurcate distally for up to half their length, and have as many as 35 joints. The four anterior rays of the ventral lobe bear fringing fulcra. The dorsal lobe is unusual in that it is subdivided. The 6 anterior rays originate from an epaxial position. The 3 anterior rays bear fringing fulcra, the fourth (and possibly also the fifth) bifurcates and the sixth bears fringing fulcra. The seventh ray has its origin at the tip of the caudal lobe (i.e. lies in the position normally occupied by the first caudal fin-ray in other redfieldiiforms) and also bears fringing fulcra.

Squamation (Fig. 30). There are 60 body transverse scale rows, each containing 30 scales in the dorsal fin region. The scales near the dorsal and ventral margins of the body are subcircular with a pronounced dorsal peg. Those nearer the lateral line become progressively larger and more rectangular. On the ventral side of the inner

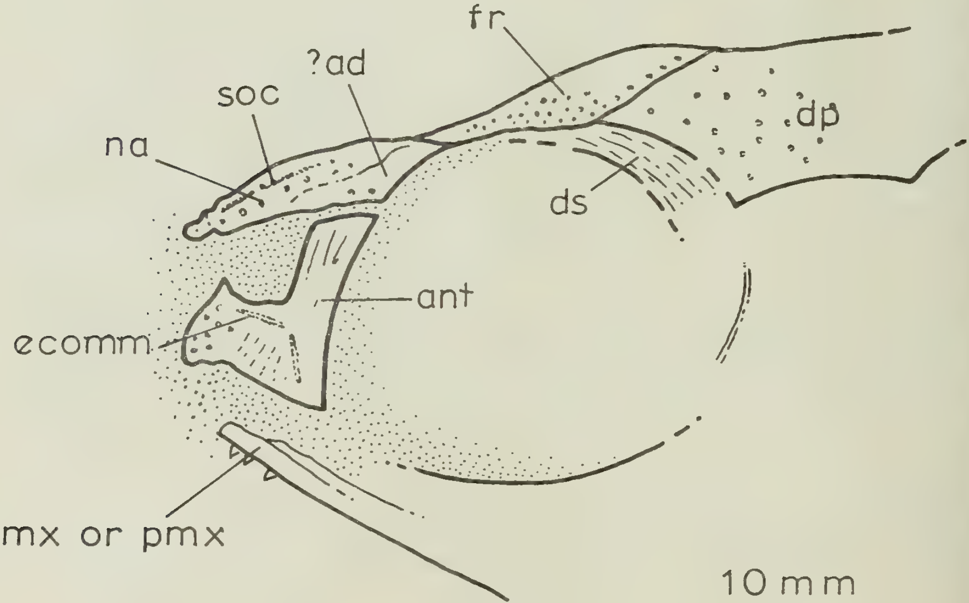

Fig. 29. *Schizurichthys pulcher* Wade. U.S.G.D. 305: left side.

surface of each scale there is a socket, into which the dorsal peg of the next ventral scale fits. All the scales are ornamented with rows of tubercles which radiate from a point near the antero-dorsal corner of the scale.

GENERA PROVISIONALLY ASCRIBED TO REDFIELDIIFORMES

Sakamenichthys germaini Lehman *et al.*

1959 *Sakamenichthys germaini* Lehman *et al.*: 179–184, text-figs 1–2, pls 1–2.

HORIZON AND LOCALITY. Scythian. Middle Sakamena group, Madagascar.

REMARKS. The reasons for including this genus in the order Redfieldiiformes are slight. The opercular series appears to consist of an opercular, a subopercular and a single branchiostegal element, but this is one of the only known features of *Sakamenichthys* which can be compared with redfieldiiform anatomy.

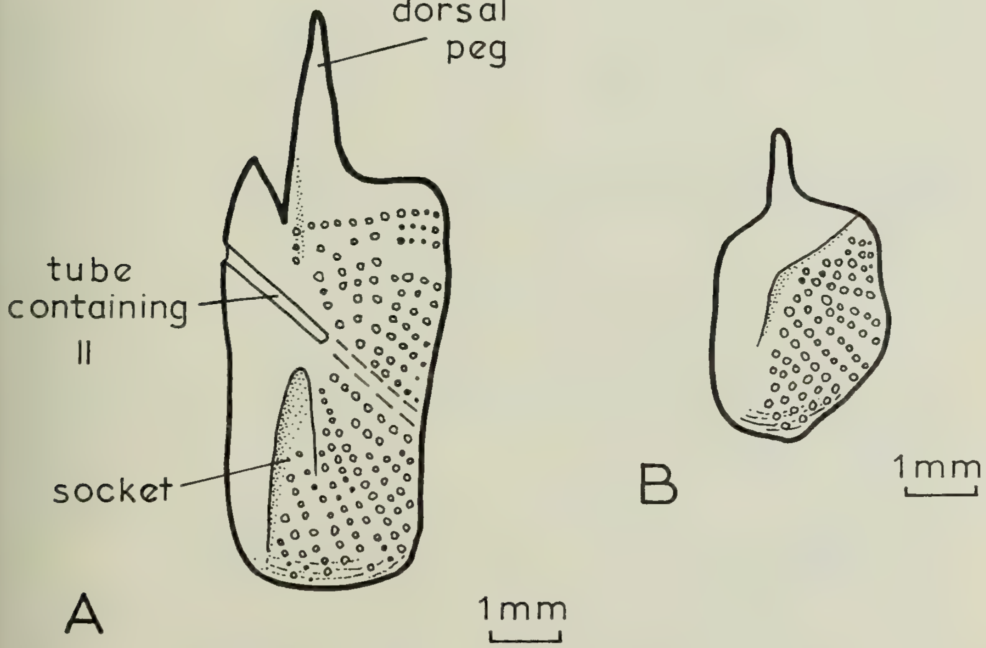

FIG. 30. *Schizurichthys pulcher* Wade. (A) P.15892: scale from anterior lateral line region, right side, internal surface. (B) P.15892: scale from ventral side of body, left side, external surface.

Sinkiangichthys longipectoralis Liu

1958 *Sinkiangichthys longipectoralis* Liu: 149–150, pl. 1.

HORIZON AND LOCALITY. Triassic. Chang-P'eng-Kon, Chitai, Sinkiang, China.

REMARKS. This genus is represented by a single specimen 98 mm long. It is poorly preserved, and the only characters noted by Liu which show that it could be a redfieldiiform are: eye forward in position; maxilla low anteriorly with a high postorbital part; heterocercal tail; no branchiostegal rays. With the exception of the last, which could be the result of poor preservation, all these characters could equally be found in other chondrostean orders.

'*Dictyopyge*' *robusta* Woodward

(Fig. 31)

1890 *'Dictyopyge' robusta* Woodward: 20, pl. 3, figs 4–5

HOLOTYPE. AM.MF 170.

MATERIAL. Holotype and AM.MF 169, P.6271a and b, and P.18110.

'*Dictyopyge*' *symmetrica* Woodward

1890 *'Dictyopyge' symmetrica* Woodward: 17, pl. 4, figs 5–6.

HOLOTYPE. AM.MF 173.

MATERIAL. Holotype and AM.MF 167, F.13394, P.6270.

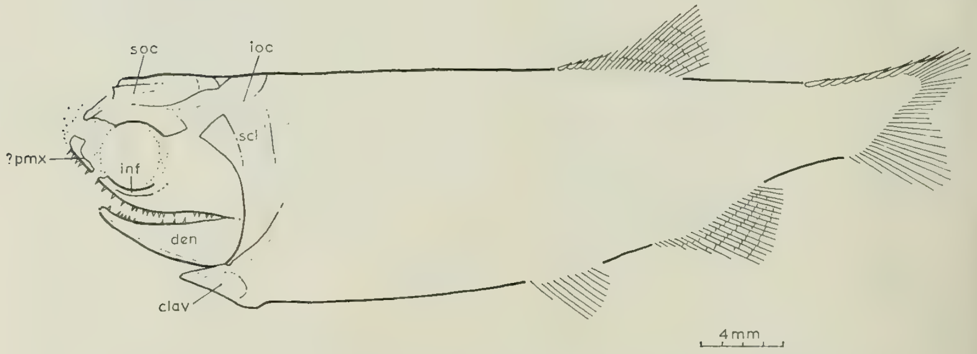

FIG. 31. *Dictyopyge robusta* Woodward. P.6271a: left side, scales omitted.

'Dictyopyge' illustrans Woodward

1890 *'Dictyopyge' illustrans* Woodward: 18, pl. 4, figs 7–9.

HOLOTYPE. In the collection of the Australian Museum, Sydney (but possibly lost. Pickett, pers. comm.).

MATERIAL. AM.MF 171, 172, F.13343, P.6269, P.18111 and P.33239.

HORIZON AND LOCALITY. Of all three species; Scythian or Anisian. Band of shale 6 feet thick at the top of the Narrabeen Shales, Gosford, N.S.W.

REMARKS. All the specimens of *'Dictyopyge'* from Gosford are poorly preserved and little can be added to Woodward's description of the three species (1890; 16–22). In particular, the skulls have been badly crushed and any comparison with any other fish, including the type species of the genus *Dictyopyge, D. macrura*, must be based almost entirely on features such as body form and the nature of the scales and fins.

Some characters of the Gosford 'dictyopygids' are seen also in the genus *Brookvalia*. These are:

1. Body shape. In both genera the body is fusiform. Most species are slender, with one exception, *'D'. robustus*.

2. Scales. Leaf-shaped as in *Brookvalia*, though there appear to be fewer scales in 'dictyopygids'. A well preserved body of *'D'. robusta* (P.6271a) has 33 body transverse scale rows which contain 13 scales in the dorsal fin region, compared with 50 body transverse scale rows which contain about 30 scales in the region of the dorsal fin in *Brookvalia gracilis*.

3. The unpaired fins. In both genera the unpaired fin-rays are repeatedly jointed and bear fringing fulcra. There are bifurcating rays in the tail of the holotype of *'D.' symmetrica* (AM.MF 173) but most other specimens are not well enough preserved for their identification to be certain. The position of the dorsal fin in various species of *Brookvalia* varies from level with the anal fin (*B. gracilis*) to anterior to the anal fin (*B. propennis* and *B. spinosa*). The same variation is seen in the Gosford species; the dorsal fin lies level with the anal fin in *'D.' symmetrica*, and anterior to the anal fin in *'D.' illustrans* and *'D.' robusta*.

In addition to these very general similarities between *'Dictyopyge'* and *Brookvalia*, some features of the skull of *'D.' robusta* merit brief mention. Specimen P.6271a (Fig. 31) shows that the skull length is about a quarter of the length of the entire body. The orbit is small and lies close to the edge of the upper jaw, although its border is separated from the maxilla by an infraorbital series. A notable feature is the steep upturning of the upper jaw as it curves below the orbit towards the snout. The lower jaw, although damaged at its symphysial end, appears not to reach the tip of the upper jaw tooth row. These last two characters are the strongest evidence for believing that *'D.' robusta*, at least, is allied to the Brookvaliidae.

In conclusion, therefore, there is some slight evidence to support Wade's opinion (1940 : 208) that the Gosford 'dictyopygids' are related to *Brookvalia* or a similar genus.

Pseudobeaconia bracaccinii Bordas

1944 *Pseudobeaconia bracaccinii* Bordas: 454–455, pl. 1.

Pseudobeaconia elegans Bordas

1944 *Pseudobeaconia elegans* Bordas: 456, pl. 1.

Horizon and locality. Of both species, Triassic bituminous rocks, Santa Clara, Mendoza and San Juan provinces, Argentina.

Remarks. *Pseudobeaconia* is now known to be an advanced perleidiform genus (Hutchinson, in press).

Rushlandia gilli Bock

1959 *Rushlandia gilli* Bock: 113–120, text-figs 49–51, pls 20–21.

Horizon and locality. Carnian or Norian. Lockatong formation (Newark), Fairview Village and Rushland, Pennsylvania, U.S.A.

Remarks. The general body shape, and the structure and position of the fins of *Rushlandia* do not exclude this genus from membership of the Redfieldiiformes, nor do they exclude it from possible membership of several other sub-holostean or holostean groups. The shape of the maxilla in *Rushlandia* is reminiscent of that seen in redfieldiiforms.

AN UN-NAMED SPECIMEN IN THE COLLECTION OF THE INDIAN STATISTICAL UNIT CALCUTTA

An un-named sub-holostean has been reported from the Maleri formation of India (Jain, Robinson & Chowdhury, 1964 : 118) which is possibly a redfieldiiform. This species has not yet been described. There is one fragment showing part of the posterior region of the head. This shows an opercular, a 'considerably larger' subopercular and part of the upper jaw (Jain, pers. comm.).

Order PERLEIDIFORMES

Diagnosis. See Berg 1958 : 131–132.

Family **COLOBODONTIDAE** Stensiö 1916

Diagnosis. See Schaeffer 1955 : 19, except than an antorbital is present.

Genus ***MEIDIICHTHYS*** Brough 1931

1931 *Meidiichthys* Brough: 261.

Diagnosis. See Brough (1931 : 261–262). Two slight amendments can be made to Brough's diagnosis. Firstly the opercular is shorter than the subopercular and has a convex ventral border, and the two bones consequently do not form 'one continuous quadrangular plate'. Secondly, the suture between the maxilla and preopercular is curved, hence the maxilla does not in effect come to an 'apex situated just behind the orbit'.

Type (and only) species. *Pholidophorus browni* Broom.

Remarks. There is little doubt that *Meidiichthys* is closely related to forms such as *Perleidus* (Stensio 1932; Lehman 1952). Specializations of the genus include the presence of a forwardly directed suspensorium and a large flat post-rostral (Brough 1931 : 262). Also the small number of branchiostegals in *Meidiichthys* should be noted here. One feature, however, suggests that the genus is close to the basal stock of all perleidids; this is the presence of a clavicle (G.N. 312, Fig. 33). In many perleidids the clavicle is small or absent.

Meidiichthys browni (Broom)

(Figs 32–33)

1909 *Pholidophorus browni* Broom: 267–268, pl. 13, fig. 10
1931 *Meidiichthys browni* (Broom) Brough: 262–266, text-figs 11–12, pl. 4, fig. 1.

Horizon and locality. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis. As for the genus *Meidiichthys*.

Holotype. S.A.M. 6030.

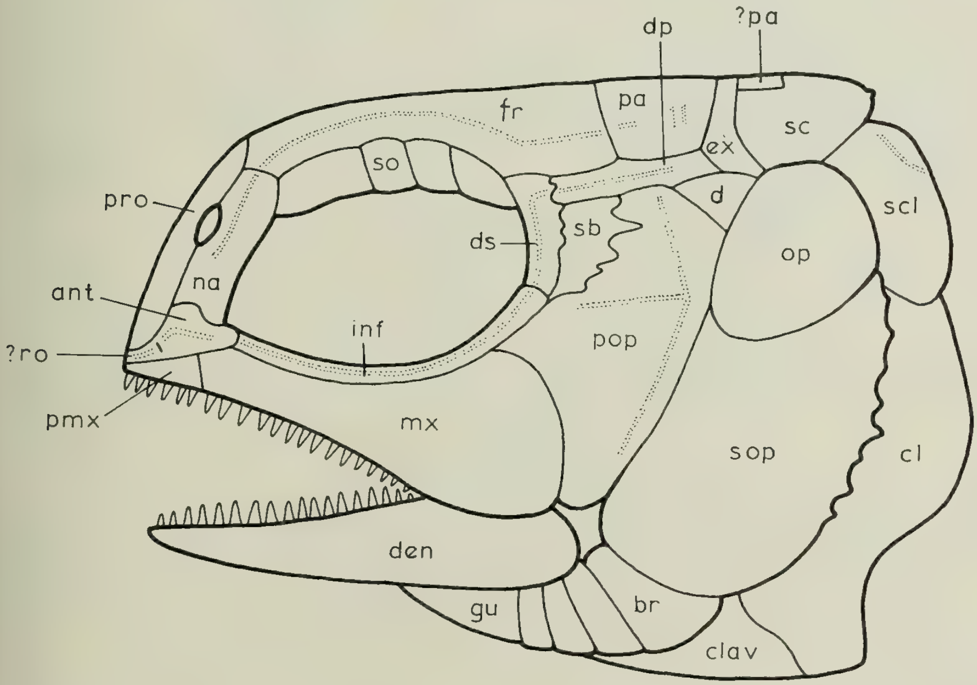

Fig. 32. *Meidiichthys browni* (Broom). Restoration of skull and pectoral girdle, ×5 approx.

MATERIAL. P.16074, P.16075, G.N. 304 and counterpart 318, 305, 311–314, 317, 348 and counterpart 355.

DESCRIPTION. *M. browni* has been described by Brough (1931 : 262–266). A new restoration of the skull is given here (Fig. 32) to include additions and amendments.

The opercular has a curved ventral border (G.N. 312, Fig. 33); the posterior border of the subopercular is pectinated and its surface ornamented with small spines. The preopercular has a more strongly concave antero-ventral border than is shown in Brough's figure (1931 : text-fig. 11). In addition to the usual preopercular sensory canal, there is a long horizontal branch extending across that bone (P.16075). The single triangular suborbital and the rectangular dermosphenotic have pectinated posterior borders. The dorsal side of the orbit is bordered by four supraorbital elements (G.N. 304). These are deep and appear considerably foreshortened in the restoration.

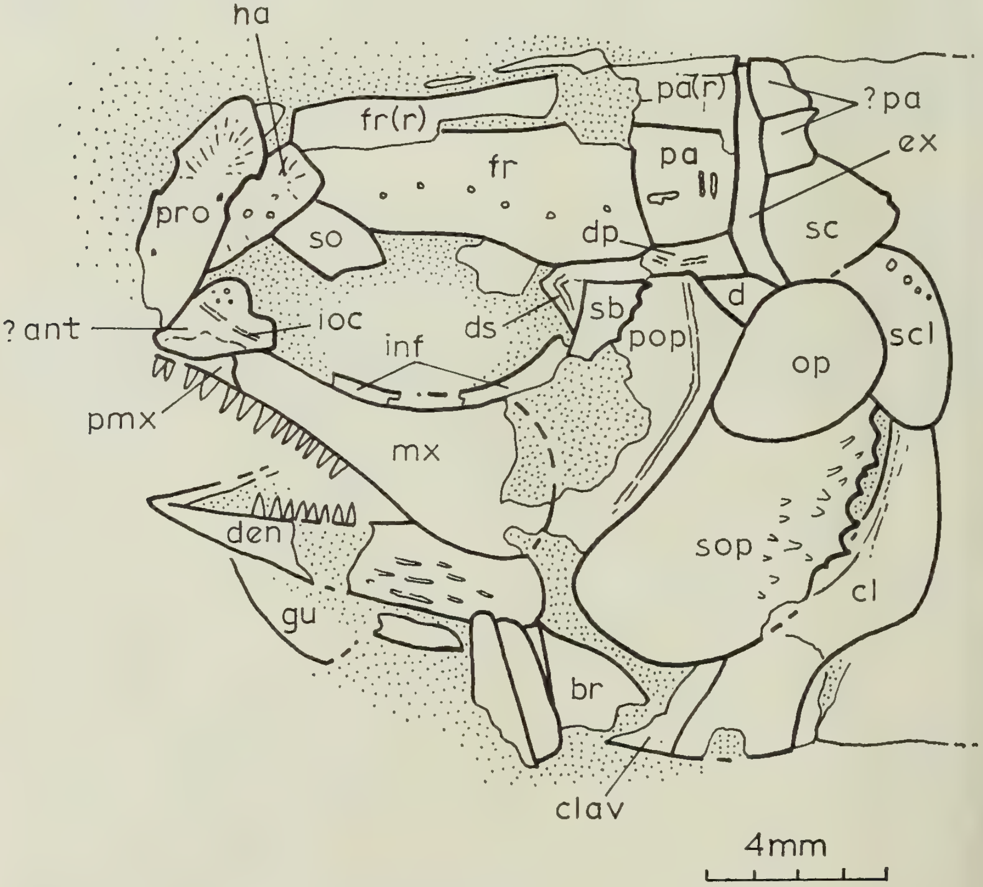

FIG. 33. *Meidiichthys browni* (Broom). G.N. 312: left side unless otherwise indicated.

The nasals are long and separated by a large postrostral (G.N. 312, Fig. 33). The nostrils lie between the anterior edges of the nasals and the lateral edges of the postrostral. The ventral part of the snout consists of an element which bears part of the infraorbital sensory canal (G.N. 312, Fig. 33) and the ethmoid commissure (P.16075). There is some indication in specimen P.16075 that the anterior part of this element is a separate bone, but this cannot be confirmed in other specimens. It is therefore uncertain whether the ventral part of the snout consists of a rostro-antorbital or of separate rostral and antorbital bones.

The anterior end of the upper jaw is composed of small wedge-shaped premaxillae. There are four branchiostegal rays.

The suprascapulars are the normal 'D' shape, but do not meet in the midline and are separated by a pair of small square elements (G.N. 312, Fig. 33). The identity of these elements is uncertain, although they are similar in shape to the posterior parietals seen in some specimens of *Perleidus piveteaui* (Lehman 1952 : text-fig. 88B). The suture between the cleithrum and clavicle is seen in specimen G.N. 312 (Fig. 33).

Genus ***PROCHEIRICHTHYS*** Wade 1935

1935 *Procheirichthys* Wade: 62.

Diagnosis. As in Wade 1935 : 62.

Type (and only) species. *Procheirichthys ferox* Wade.

Remarks. Little can be added to the description made by Wade of this incompletely known genus except that the nasal is not separated from the orbital border.

Procheirichthys ferox Wade
(Fig. 34)

1935 *Procheirichthys ferox* Wade: 62–64, text-fig. 31, pl. 9, fig. 2.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. As for the genus *Procheirichthys*.

Holotype. U.S.G.D. 209, the only known specimen.

Description. *Size* (Fig. 34). *P. ferox* is a fairly deep-bodied fish with a deep, short skull. Its total length from snout tip to the posterior end of the caudal fin is 163 mm. The greatest body depth occurs about midway between the pectoral region and the anterior edge of the dorsal fin.

Skull (Fig. 34). The skull is deep, and the roof curves evenly to the snout so that its overall shape is triangular. The extrascapular is narrow and the parietal rectangular, being deeper than long. The frontal is extremely deep and fairly short. Neither the suture between the dermopterotic and the extrascapular, nor that between the anterior end of the dermopterotic and the dermosphenotic are preserved. The suture between the opercular and subopercular is indistinct, but appears to divide the opercular plate so that the subopercular is almost twice as deep as the opercular. The angle between the anterior margin of the opercular series and the ventral margin of the maxilla is 72°, but in fact the opercular series is orientated almost vertically and the ventral edge of the maxilla slopes anterodorsally towards the snout tip. The preopercular appears to be broad, and dermohyal, suborbital and infraorbital elements are either absent or not preserved. The dorsal side of the orbit is bordered by three small supraorbitals.

The snout is not complete, but appears to be similar to that of *Mendocinia* (Schaeffer 1955). The nasal is rectangular and is not separated from the anterior border of the orbit as suggested by Wade (1935 : text-fig. 31). There is a fragment of bone lying anterior to the dorsal end of the nasal which is probably part of the postrostral. The ventral part of the snout is divided by a vertical suture which runs from the ventral side of the nasal to the margin of the upper jaw. Crossing this suture there is a short sensory canal. Although no more of the snout is preserved, it is probable that there were antorbital and rostral elements lying ventral to the nasal, separated by this vertical suture. Further ventrally, the vertical suture probably separates premaxilla from maxilla. Thus the known facts are quite consistent with a snout pattern similar to that of *Mendocinia*.

The lower jaw is extremely deep, its length being only 2·5 times its maximum depth. The teeth are large, conical and pointed.

Pectoral girdle. The dorsal part of the pectoral girdle is not well preserved but there are indications that the suprascapular elements are well separated and do not meet in the midline. The cleithrum is ornamented with fine parallel ridges.

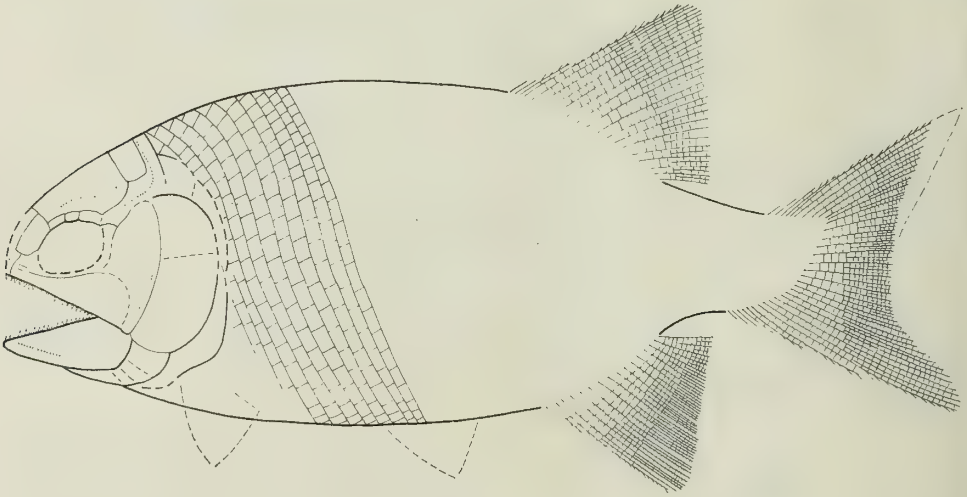

FIG. 34. *Procheirichthys ferox* Wade. Restoration, ×0·8 approx. Posterior scales omitted.

Paired fins. The paired fins are not preserved in *Procheirichthys*.

Unpaired fins. All the unpaired fin-rays bifurcate distally, and the leading rays bear fringing fulcra. The anal fin has 18 rays which bifurcate twice, and there are up to 23 joints.

The dorsal fin contains 20 rays which bifurcate once. The anterior rays bear fringing fulcra and there are up to 18 joints.

The body lobe of the tail is very abbreviated. The caudal fin has 34 rays, 18 in each lobe. Ten rays in the dorsal lobe are epaxial in position. Most bifurcate twice and there are up to 30 joints.

Squamation. The scales are smooth and rhombic. There are 42 transverse body scale rows, not including any in the region immediately posterior to the cleithrum, where none are preserved.

Genus ***MANLIETTA*** Wade 1935

1935 *Manlietta* Wade: 58.

DIAGNOSIS (emended). Skull short and deep, 25% of total body length with head. Skull bones smooth or ornamented with fine granular tubercles. Rostrum sloping as in *Mendocinia*. No postrostral. Nasals forming anterior border of orbit and meeting in the midline. Nostril at ventral border of nasal. Snout composed of rostral, paired antorbitals and probably premaxillae. Frontals three times as long as the square parietals. Dermopterotic narrow and elongate. Suspensorium steeply inclined. Wedge-shaped dermohyal present. Preopercular divided into two ossifications, lower element with infraorbital process. No suborbital. Opercular equal in size to subopercular. Three or four branchiostegals present. Gular almost as long as lower jaw. Mandible stout and tapering anteriorly. Teeth large and well separated.

Body deeply fusiform, with greatest depth immediately behind pectoral girdle. Paired fins poorly preserved but pectoral fin containing at least 8 rays, and pelvic fin at least 6 rays. Unpaired fins with fringing fulcra, bifurcating rays and basal fulcra. Anal and dorsal fins posterior in position, dorsal fin slightly in advance of anal. Anal fin with 9 long rays, dorsal fin with 17 rays. Caudal fin hemiheterocercal, slightly cleft, equilobate and with 17 rays. Scales smooth with straight posterior borders.

TYPE (and only) SPECIES. *Manlietta crassa* Wade.

REMARKS. *Manlietta* is extremely similar to *Mendocinia* from Argentina. Of the characters listed by Schaeffer (1955 : 4) in the generic diagnosis of *Mendocinia*, the following important similarities with *Manlietta* may be noted: rostrum sloping rather than blunt; nasal bones forming anterior border of orbit; paired dentigerous premaxillaries; dermopterotic narrow and elongated; preopercular with infraorbital process; teeth conical; dorsal fin remote, origin midway between origin of pelvic and anal fins; caudal fin hemiheterocercal, moderately cleft and equilobate; anterior scales thin, smooth with straight posterior border, decreasing in depth posteriorly. Many of these features are common to all perleidids but, overall, the similarity between the two genera is impressive (cf. Fig. 35 and Schaeffer 1955 : text-fig. 1). The differences between the cheek regions of *Manlietta* and *Mendocinia* can be related to the fact that the suspensorium is more vertical in the latter. This difference is accompanied by a reduction in the width of the preopercular, and considerable reduction of the posterior part of the maxilla. Other changes can be seen in the anatomy of the fins. In *Manlietta* the unpaired fins bear fringing fulcra, but these are lost in *Mendocinia*; also, whereas in *Manlietta* the basal fulcra of the anal and dorsal fins do not exceed the length of the proximal lepidotrichia, in *Mendocinia* they extend almost to the distal ends of the anterior rays.

There are several reasons for supposing that, although closely related, *Manlietta* is not ancestral to *Mendocinia*. The preopercular of *Manlietta* is subdivided and there is no postorbital element, and the anal fin-rays are unusually long. More important is the anatomy of the snout. In *Manlietta* the postrostral has been lost and the nasals meet in the midline. In consequence the nostril cannot lie at the anterior margin of the nasal, and is situated at the ventral edge of the nasal. This condition is paralleled in *Birgeria* and *Haplolepis*, although in these forms the postrostral is still present, and reasons for migration of the nostril from the position more typical of lower actinopteryians are obscure.

Manlietta crassa Wade
(Figs 35–37)

1935 *Manlietta crassa* Wade: 59–62, text-figs 29–30, pl. 9, fig. 1.

Horizon and locality. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

Diagnosis. As for the genus *Manlietta*.

Holotype. U.S.G.D. 213.

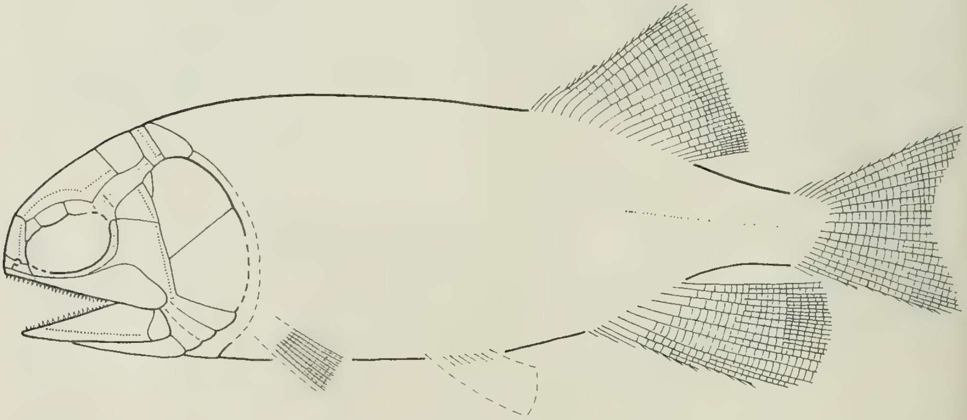

Fig. 35. *Manlietta crassa* Wade. Restoration, ×2 approx. Scales omitted.

MATERIAL. Holotype and P.15881 and counterpart P.16825.

DESCRIPTION. *Size* (Fig. 35). The total length from snout tip to the posterior end of the caudal fin is 77 mm (P.15881). The greatest body depth occurs immediately behind the pectoral region.

Skull (Fig. 36). The skull is similar to that of *Mendocinia brevis* from the Triassic of Argentina (Schaeffer 1955 : text-fig. 4). The edge of the frontal which borders the dermopterotic is concave in *Manlietta* (U.S.G.D. 213, Fig. 37), whereas it is convex in *Mendocinia*. The supraorbital sensory canal closely follows the ventral edge of the frontal and is straight posteriorly and curved over the orbital region. The dermopterotic is shallow and rectangular, and does not extend dorsally between

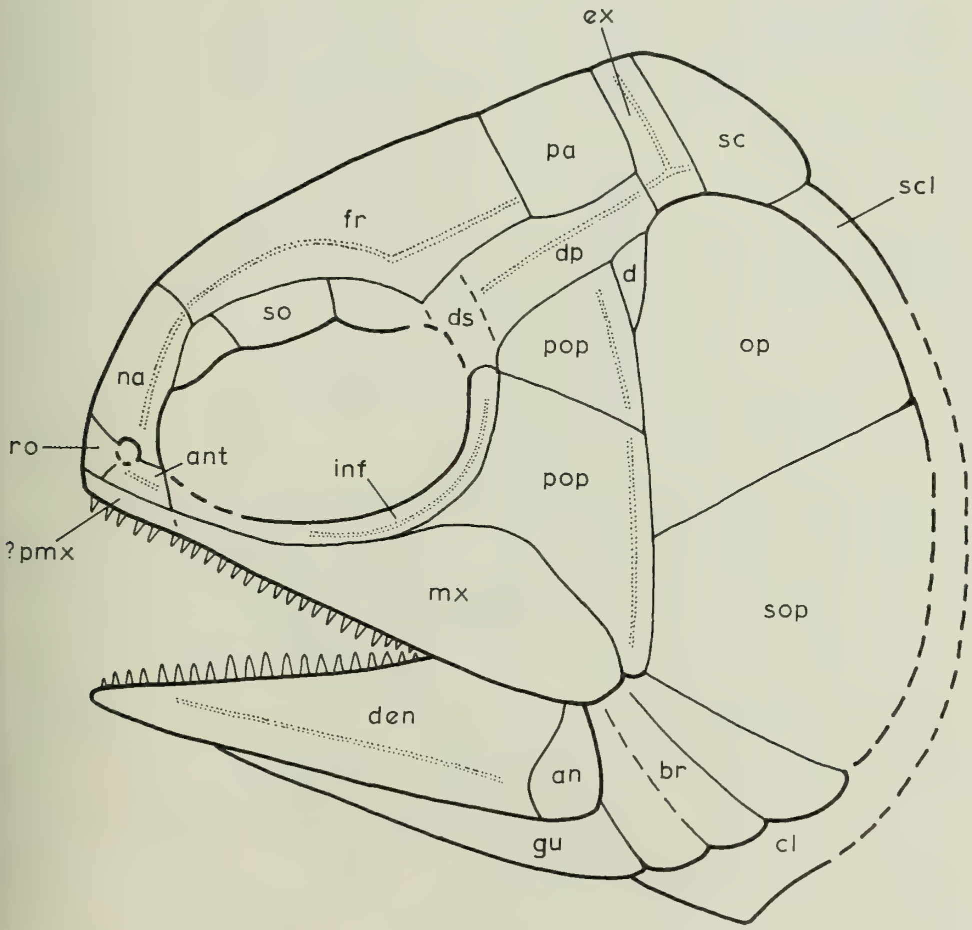

FIG. 36. *Manlietta crassa* Wade. Restoration of skull and pectoral girdle, ×7 approx.

the frontal and parietal. There is no evidence that the skull roof in *Manlietta* is separate from the cheek region along the ventral edge of the dermopterotic as it is in *Mendocinia*. The dermosphenotic is not preserved. The overall shape of the opercular plate is similar to that of *Mendocinia*. In *Manlietta*, however, the suture dividing the opercular and subopercular slopes postero-dorsally so that the two bones have a similar surface area. The angle between the anterior edge of the opercular series and the ventral border of the maxilla is 82° in *Mendocinia*, and 64° in *Manlietta*. A wedge-shaped dermohyal is present in *Manlietta* (U.S.G.D. 213, Fig. 37) but this does not extend as far ventrally along the anterior margin of the opercular as it does in *Mendocinia*. In *Manlietta* there are three branchiostegal rays. The gular plate is extremely long and extends below the entire length of the lower jaw.

In *Manlietta* the preopercular is broad and there is no sign of any suborbital (supraspiracular) element. In one specimen (U.S.G.D. 213, Fig. 37) a suture divides the preopercular into two elements. The ventral preopercular element is characterized by a narrow extension passing antero-ventrally between the maxilla

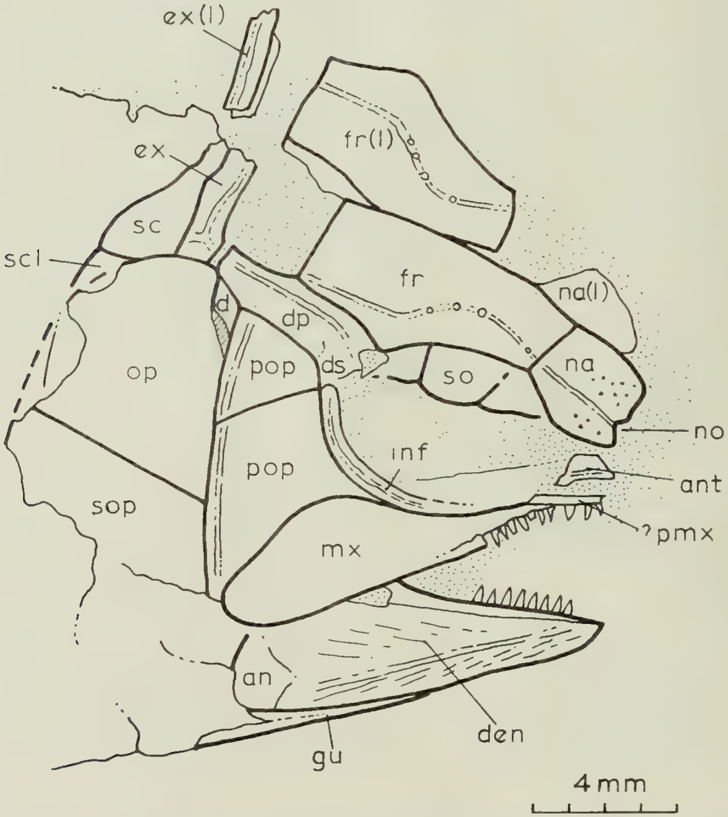

FIG. 37. *Manlietta crassa* Wade. U.S.G.D. 213: right side unless otherwise indicated.

and the infraorbital elements. The length of the cheek region is greater in *Manlietta* than in *Mendocinia* so that the posterior part of the maxilla in the former genus appears to be much more shallow. In fact the dorsal extent of the maxilla is similar in both genera. In specimen U.S.G.D. 213 (Fig. 37) there is a break at a point where the suture between the maxilla and a premaxilla may well have been present. The teeth of the upper jaw are large and somewhat blunt.

The infraorbital elements are narrow. The dorsal side of the orbit is bordered by three irregularly shaped supraorbitals, the centre member being the largest.

The snout region of *Manlietta* is not only different from that of *Mendocinia*, but also from all other perleidids in which this region is known. The nasals are ornamented with fine tubercles, are broad and meet in the midline, there being no postrostral. The nostril is situated on the ventral margin of the nasal (P.16825 and U.S.G.D. 213, Fig. 37). Ventral to the nasal there is a small rostral (P.16825) and a tetragonal antorbital which bears part of the infraorbital sensory canal. The fact that the rostral and antorbital elements are separate in *Manlietta* makes it likely that the anterior infrorbital of *Mendocinia* (Schaeffer 1955 : text-fig. 4 B), is wrongly identified, and is in fact an antorbital element. This view is supported by the fact that this bone bears the Y-shaped division of the infraorbital sensory canal.

Lower jaw. The lower jaw of *Manlietta* is stout. It is deep posteriorly and tapers to a blunt point. The dentary is ornamented with elongate rugae. The suture between the dentary and the angular is clearly seen in specimen U.S.G.D. 213 (Fig. 37). The dentary teeth are large, blunt and well separated.

Paired fins. The pectoral fins are poorly preserved in specimen U.S.G.D. 213. There are at least 8 rays which bifurcate and which have up to 11 joints.

The pelvic fin consists of at least 6 rays, but no details are preserved.

Unpaired fins. The anal fin has 9 rays which are so long that they extend posteriorly beyond the anterior edge of the caudal fin. The posterior rays bifurcate twice. The anterior rays bear fringing fulcra and there are up to 21 joints. The proximal joints are 4–5 times as long as those lying more distally (in *Mendocinia* they are 6–7 times as long and extend further distally).

The dorsal fin has 17 rays which have between 8 and 15 joints. The anterior rays bear fringing fulcra.

The caudal fin is almost homocercal, is slightly cleft and equilobate. There are 17 rays which are widely spaced, especially at the centre of the tail. The anterior rays of both the dorsal and ventral lobes bear fringing fulcra. All the rays are bifurcated and there are up to 20 joints.

Anterior to each unpaired fin there are basal fulcra, the longest of which are equal in length to the most proximal joints of the anterior fin-ray.

Squamation. The scales in the anterior part of the body are not well preserved but appear to be rhomboidal. Further posteriorly they become leaf-shaped. There is no surface ornament. There are about 36 body transverse scale rows.

Family **CLEITHROLEPIDIDAE** Wade 1935

Diagnosis. Head deep posteriorly. Bones ornamented with tubercles. Parietal square. Frontal elongate and moderately deep. Accessory dermopterotic present. Opercular series vertical or almost vertical. Opercular smaller than subopercular. Small triangular dermohyal present. Quadratojugal present. Ventral end of preopercular narrow above quadratojugal. Preopercular with antero-ventral process. Three supraorbital elements present. Paired nasals separated by a postrostral. Nasal probably separated from the orbit margin. Paired 'Y'-shaped rostro-antorbitals or, possibly, separate rostrals and antorbitals. Premaxillae probably always present. Lower jaw slender and finely tapered. Teeth very small or absent.

Body deep, dorsal side with marked hump, ventral side strongly convex. Suprascapular absent. Accessory dermopterotic separating the extrascapular from the dorsal border of the opercular. Postcleithrum probably present. Rays of paired fins jointed or unjointed, sometimes bifurcated. Unpaired fin-rays jointed many times, bifurcating. Anterior rays of each fin bearing fulcra and more numerous than their endoskeletal supports, posterior rays more widely spaced. Dorsal and anal fins situated close to the caudal fin so that their anterior rays lie well posterior to the deepest part of the body. Short body lobe in tail. Scales elongate and ornamented with fine tubercles. Scales in pectoral region orientated antero-ventrally.

Genus ***CLEITHROLEPIDINA*** Berg 1940

1940 *Cleithrolepidina* Berg: 405.

The genus *Cleithrolepidina* was erected by Berg (1940 : 405) to include *Cleithrolepis minor* Broom, which he thought had a more vertical suspensorium than other members of the genus *Cleithrolepis*. The cheek region of *C. minor* has been reexamined and there appears to be no significant difference between the two genera in this respect. However, there are three other differences between the two genera. In *Cleithrolepidina* the maxilla is extremely shallow anteriorly, the snout is only moderately deep and the extrascapular is undivided. In *Cleithrolepis*, on the other hand, the maxilla is very deep throughout its length, the snout is extremely deep and the extrascapular is divided. Thus the genus *Cleithrolepidina* is valid, but not on Berg's grounds.

Diagnosis (emended). Deep-bodied fish similar to *Cleithrolepis*, but in which the skull is moderately deep. The maxilla tapers anteriorly, and its anterior half is extremely shallow. Premaxilla very small or absent. Snout moderately deep, so that the nasal is roughly 3 times as deep as it is long. Postrostral half as long as the frontal. Extrascapular undivided.

Type species. *Cleithrolepis minor* Broom.

Cleithrolepidina minor (Broom)
(Figs 38–39)

1909 *Cleithrolepis minor* Broom: 266, pl. 13, fig. 9.
1931 *Cleithrolepis minor* Broom; Brough: 267–270, text-fig. 13.
1940 *Cleithrolepidina minor* (Broom) Berg: 405.

HORIZON AND LOCALITY. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

DIAGNOSIS (emended). Parietal almost rectangular with straight ventral edge. Dermopterotic narrow and rectangular. Opercular with straight ventral edge. About five branchiostegal rays. Preopercular rounded dorsally, the dermohyal and suborbital being small. Anterior process of preopercular overlapped by postero-dorsal border of maxilla. Maxilla with a postero-dorsal extension running behind posterior infraorbital. Posterior supraorbital equidimensional. Teeth probably absent.

Supracleithrum in contact dorsally with accessory dermopterotic and with extrascapular.

HOLOTYPE. S.A.M. 6037.

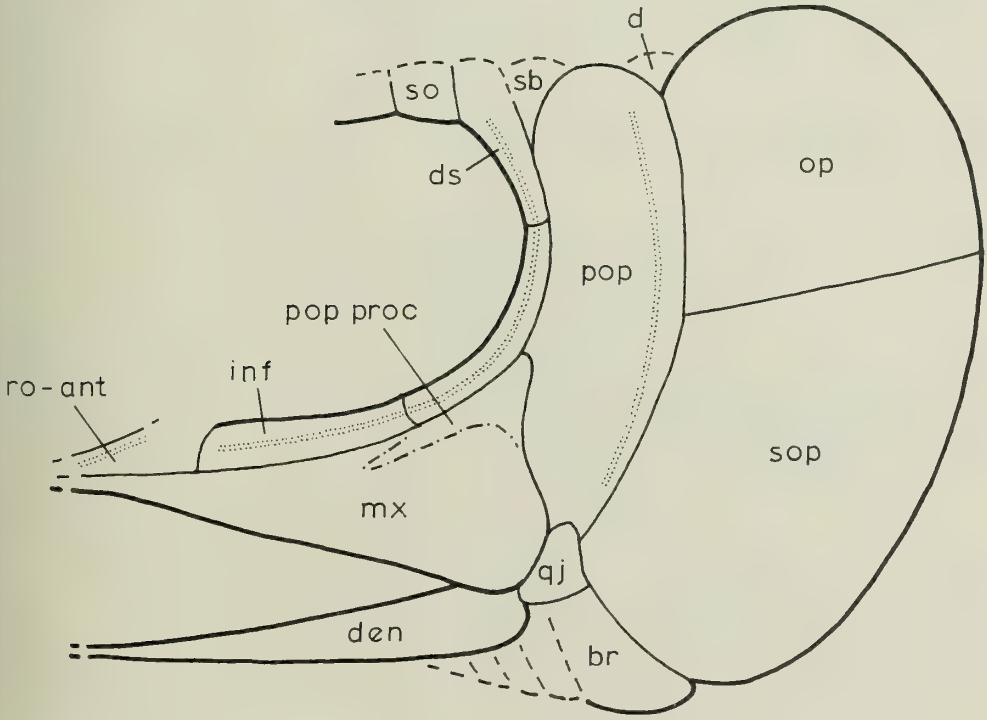

FIG. 38. *Cleithrolepidina minor* (Broom). Restoration of jaws, cheek and opercular regions, ×8 approx.

MATERIAL. P.12594, P.16048–51, P.16067, P.16068 and counterpart P.16069. G.N. 293, 194, 328, 330 and counterpart 331.

DESCRIPTION. This species has been well described by Brough (1931 : 267–270) and little can be added here. However, the species has been placed in a new genus *Cleithrolepidina* by Berg (1940 : 405) because it was thought to have a vertical rather than an inclined supensorium. A description of the cheek region of *C. minor* is therefore given here in order to assess the validity of this taxonomic change.

Cheek region (Fig. 38). The maxilla, preopercular and opercular bones are well preserved in specimens G.N. 330 (Fig. 39) and its counterpart G.N. 331. The opercular is as long as it is broad. The suture between it and the subopercular is straight and slightly inclined postero-dorsally. The subopercular is almost 1·5 times the depth of the opercular. Four or five branchiostegal rays are present. The angle

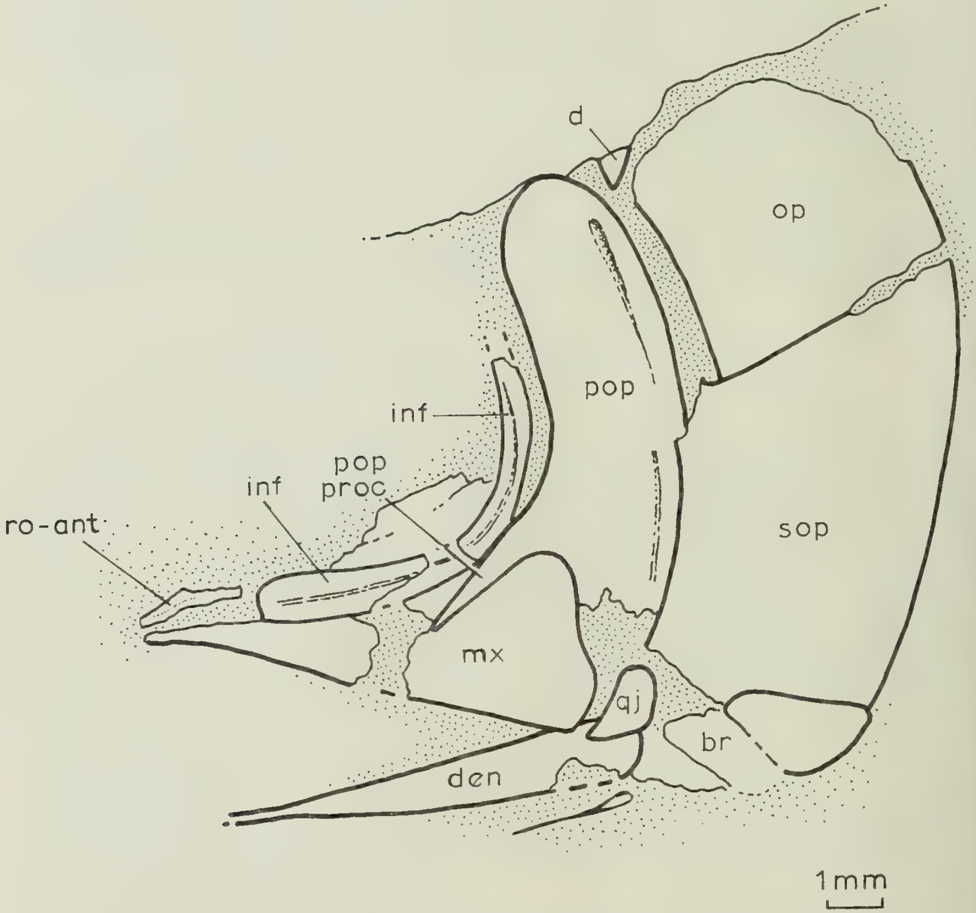

FIG. 39. *Cleithrolepidina minor* (Broom). G.N. 330: right side, internal surface.

between the anterior edge of the opercular series and the ventral edge of the maxilla is 86°.

The preopercular is kidney-shaped. Its posterior edge is convex, fitting closely to the anterior margin of the opercular series; its dorsal end is rounded and not constricted between the suborbital and dermohyal as it is in *C. extoni* and *C. granulata,* although dermohyal and suborbital are present (G.N. 331, P.16048 and P.12594). Its anterior edge is concave, the dorsal part bordering the posterior infraorbital and the ventral part having long sinuous contact with the maxilla. The preopercular has an antero-ventrally directed process which lies below the postero-dorsal part of the maxilla. The maxilla is deep posteriorly and tapers sharply anteriorly. There is a roughly triangular quadratojugal ossification, between the maxilla and the antero-ventral corner of the subopercular (G.N. 330, Fig. 39).

Remarks. The above description shows that Berg's (1940 : 405) separation of *C. minor* from members of the genus *Cleithrolepis* on account of its more vertical suspensorium is unjustified. An accurate measurement of the angle between the anterior margin of the opercular series (a line joining the antero-dorsal corner of the opercular with the antero-ventral corner of the subopercular) and the ventral border of the maxilla may not be a measurement of the actual angle of the suspensorium, but it is closely related to that feature and, as long as the maxilla does not show too much variation, it is a useful comparative measurement. The figures obtained are:

C. granulata	93°
C. extoni	89°
C. minor	86°

Far from having a more vertical suspensorium, *C. minor* has one more inclined than either *C. granulata* or *C. extoni*.

Cleithrolepidina extoni (Woodward) comb. nov.

(Figs 40–42)

1888 *Cleithrolepis extoni* Woodward: 141–143, pl. 6, figs 6–7.
1895 *Cleithrolepis extoni* Woodward; Woodward: 156–157.
1909 *Cleithrolepis extoni* Woodward; Broom: 264–266.

This species displays the three characters which are diagnostic of the genus *Cleithrolepidina*, and has been removed to that genus.

Horizon and locality. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis (emended). Dermopterotic more or less rectangular. Opercular almost circular with strongly convex ventral edge. Three to five branchiostegal rays. Preopercular constricted dorsally between a dermohyal and a suborbital; with an anterior process running between the maxilla and infraorbital, not overlapped by the maxilla. Posterior supraorbital twice as long as it is deep. Teeth probably absent.

Supracleithrum in contact dorsally with accessory dermopterotic only.

Holotype. P.5455.

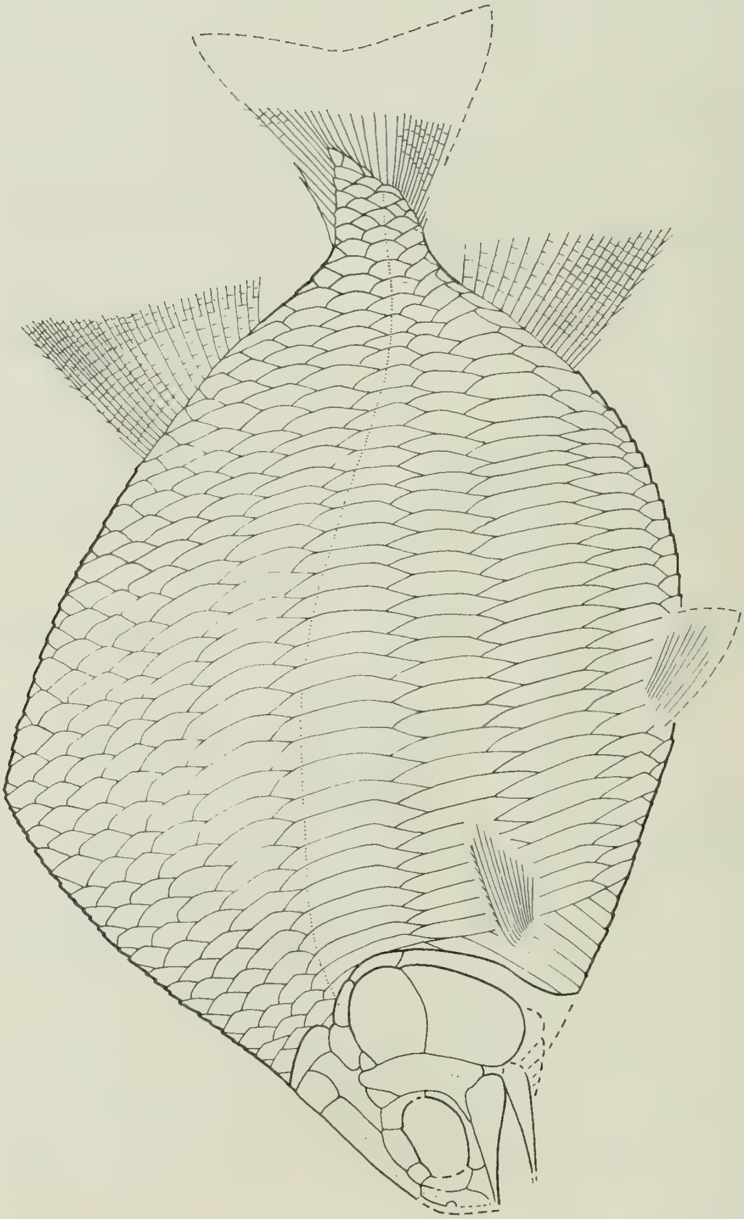

FIG. 40. *Cleithrolepidina extoni* (Woodward). Restoration, × 1·5 approx.

MATERIAL. Holotype and P.5455a, P.16043 and counterpart P.16044, P.16045, P.16105 and counterpart P.16106.

DESCRIPTION. *Size* (Fig. 40). The holotype is about 120 mm long, measured from snout tip to the posterior end of the caudal fin, and 68 mm at its greatest depth. The body is similar in shape to *Cleithrolepis granulata* (Fig. 43) in that the dorsal side of the body is humped, with a distinct point separating the anterior part of the body outline, which is convex and faces antero-dorsally, from the posterior part which is also convex and which faces postero-dorsally. The maximum body depth is almost eight times the depth of the caudal peduncle.

Skull (Fig. 41). All the dermal elements of the skull are ornamented with numerous, well defined tubercles. The head is roughly triangular, the skull roof sloping

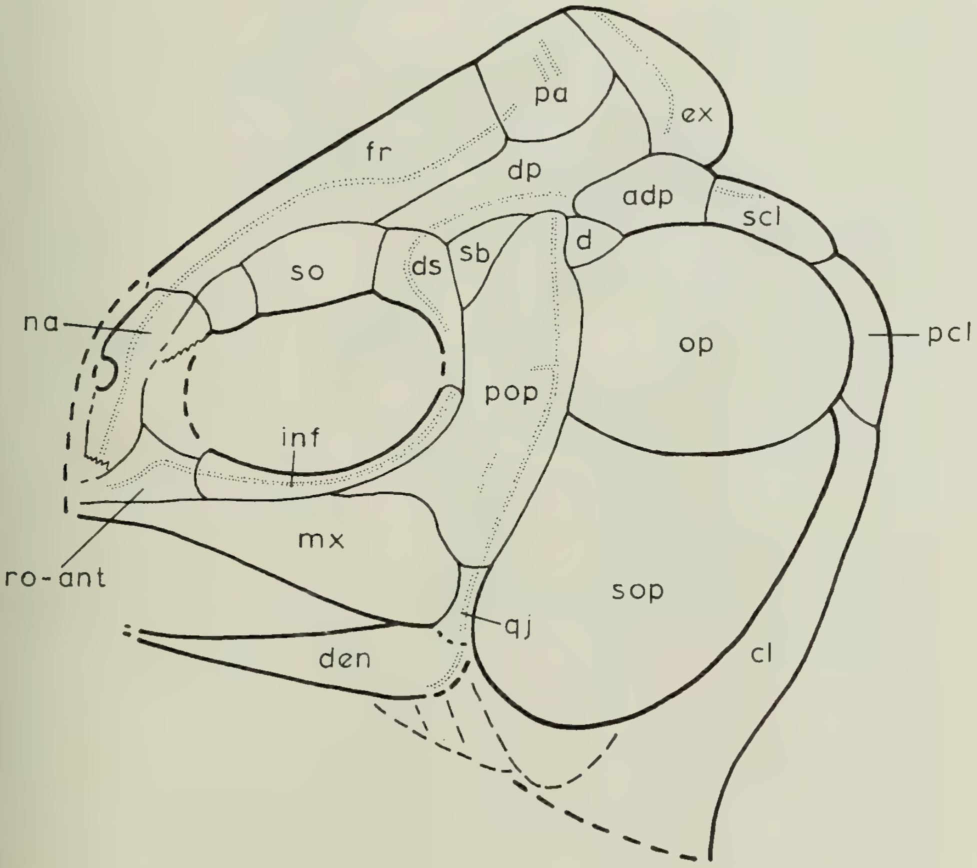

FIG. 41. *Cleithrolepidina extoni* (Woodward). Restoration of skull and pectoral girdle, ×4·5 approx.

steeply towards the snout. The supraorbital sensory canal is enclosed in a massive tube which runs along the entire length of the frontal bone. Anteriorly it is curved so that it runs parallel with the ventral border of the frontal, posteriorly it just extends on to the parietal (P.5455a). Posterior to the parietal there is a deep, narrow bone which is 'D'-shaped. This element is similar in shape to the suprascapular of many actinopterygians, but is identified as an extrascapular because it bears

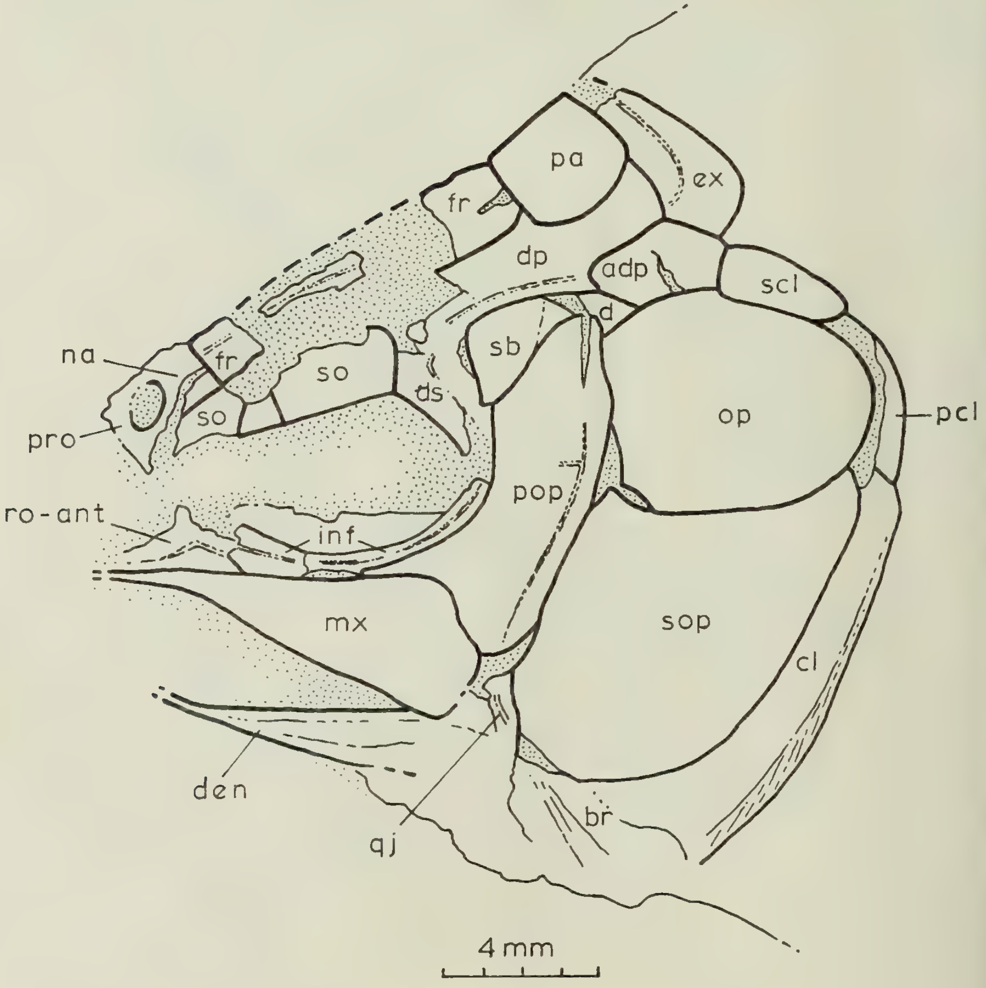
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Fig. 42. *Cleithrolepidina extoni* (Woodward). P.16045: left side. Ornament of fine tubercles omitted.

a vertical branch of the temporal sensory canal (P.16045, Fig. 42). The dermopterotic is elongate and narrow, except posteriorly where it extends dorsally between the parietal and the extrascapular.

The remaining element of the skull roof is roughly oval in shape. Dorsally it meets the postero-ventral edge of the dermopterotic and the ventral edge of the extrascapular, ventrally it meets the dorsal edge of the dermohyal (P.16045, Fig. 42). Posteriorly this element butts against the supracleithrum. In *C. minor* an element with exactly these spatial relationships bears part of the infraorbital sensory canal and is there identified as an accessory dermopterotic (see discussion of the family Cleithrolepididae, p. 338).

The opercular is slightly longer than deep and is 'D'-shaped. The subopercular is 1·3 times as deep and almost exactly the same width as the opercular. In specimen P.16045 (Fig. 42) branchiostegal rays are very poorly preserved, but there appear to be only three or four such elements. There is a small triangular dermohyal at the antero-dorsal corner of the opercular (P.16045, Fig. 42).

The dorsal end of the preopercular is constricted between the suborbital anteriorly and the dermohyal posteriorly. The ventral end of the preopercular is characterised by a narrow process which extends anteriorly between the maxilla and the infraorbital series. At the ventral end of the preopercular there is a small quadratojugal.

A short pit-line groove runs parallel with the ventral part of the preopercular sensory canal. There is a suborbital element lying anterior to the dorsal part of the preopercular, and although its external shape is triangular, it extends posteriorly for a short distance beneath the preopercular (P.16045, Fig. 42). The part of the suborbital which was overlapped is devoid of surface ornament.

The maxilla is moderately deep posteriorly, and tapers evenly towards the snout. The anterior part of the maxilla is bent ventrally in specimen P.16045 (Fig. 42) but this may be the result of post mortem distortion. Maxillary teeth were not observed.

The dermosphenotic is seen in specimen P.16043 although its ventral portion is not preserved. The posterior supraorbital is large and roughly rectangular, though with a convex dorsal border (P.16045, Fig. 42); this same element is broken in specimen P.16043. Anterior to this there are two smaller supraorbitals, the first being roughly square (P.16043). The anterior supraorbital is poorly preserved. Dorsally it meets the nasal (P.16045, Fig. 42), but as its ventral part is not preserved, it cannot be determined to what extent it borders the anterior margin of the orbit. The anterior infraorbital, or the anterior part of the anterior element, is slightly expanded.

The snout of *C. extoni* is poorly preserved. The dorsal part of the nasal is seen in specimen P.16045 (Fig. 42) where it meets the anterior part of the frontal and the dorsal part of the anterior supraorbital. A more complete nasal is preserved in the counterpart of P.16043, P.16044, and when the outline of this bone was used to restore the snout region, its ventral edge was found to coincide exactly with the dorsal edge of the ventral part of the snout as preserved in specimen P.16045. The position of the nostril is seen in both specimens P.16044 and P.16045, but although its anterior border is presumably formed by a postrostral, this bone is not clearly preserved in any specimen.

Only a single element of the ventral part of the snout can be determined. It is poorly preserved but is roughly triangular, its posterior part meeting the anterior infraorbital, and its ventral part lying above the anterior tip of the maxilla. As noted above, restoration of the snout suggests that the dorsal margin of this element was in contact with the nasal. This bone bears the anterior part of the infraorbital sensory canal, and is probably the rostro-antorbital (see Gardiner 1963 : 312).

The lower jaw is slender and probably toothless.

Pectoral girdle. The pectoral girdle is best preserved in specimen P.16045 (Fig. 42). There is no suprascapular. The supracleithrum is small and lies almost horizontally above the opercular. Anteriorly it butts against the accessory dermopterotic. The supracleithrum does not meet the cleithrum; between these bones there is a postcleithrum which is curved and which follows the posterior outline of the opercular. Only the dorsal part of the cleithrum is preserved. The posterior border of the cleithrum is ornamented with deep parallel ridges which run along the long axis of the bone. The major part of the cleithrum, however, is smooth. The clavicles, if present, are not preserved.

Paired fins. The pectoral fin contains 12 rays, the first of which bears fringing fulcra. No specimen showed any evidence of jointing or bifurcation of the rays. The pectoral fin does not lie close to the ventral margin of the body, and its base is orientated so that the insertion of the anterior ray lies antero-dorsally relative to that of the posterior ray.

The pelvic fin is poorly preserved and only 9 rays are present, showing neither trace of jointing or bifurcation, nor the presence of fringing fulcra.

Unpaired fins. In both the dorsal and anal fins the rays bifurcate, and the anterior rays bear fringing fulcra and are almost four times the length of the posterior rays. The posterior rays are more widely spaced than are the anterior rays. The dorsal fin-rays number about 20 and bear up to 17 joints, and the anal fin-rays number about 18 and bear up to 15 joints. In both fins the proximal joints are long compared with the more distal ones.

The proximal part of the caudal fin is preserved in a single specimen (the holotype, P.5455). There are about 26 rays.

Squamation. There are 36 transverse body scale rows. The scales are very deep, especially in the lateral line region where their depth is up to 6 times their length (this ratio takes into account only that part of the scale which is not overlapped by adjoining scales). Each scale bears a ridge along its posterior border and a surface ornament consisting of numerous tubercles. In general the transverse body scale rows pass postero-ventrally across the body; there are three exceptions, however: at the antero-ventral corner of the body, posterior to the cleithrum, there are about 9 scales orientated postero-dorsally; at the base of the dorsal fin the body scale rows become inclined so that scales immediately at the fin base, when viewed from above, run parallel to the long axis of the body. In a similar way the scale rows become anteriorly directed as they approach the base of the anal fin.

Genus ***CLEITHROLEPIS*** Egerton 1864

1864 *Cleithrolepis* Egerton: 3.
1890 *Cleithrolepis* Egerton; Woodward: 37.
1895 *Cleithrolepis* Egerton; Woodward: 154.
1931 *Cleithrolepis* Egerton; Brough: 266.
1935 *Cleithrolepis* Egerton; Wade: 49.
1940 *Cleithrolepis* Egerton; Berg: 405.

The genus *Cleithrolepis* has been diagnosed twice in recent years, but the diagnosis of Brough (1931 : 266–267) was based on a single species, *Cleithrolepis minor*, now thought to be a member of the genus *Cleithrolepidina* (see above) while that of Wade (1935 : 49) was based on *Cleithrolepis granulata*. *Cleithrolepis granulata* has many features in common with both species of *Cleithrolepidina* (*C. minor* and *C. extoni*), but differs in three important respects. The emended diagnosis of *Cleithrolepis* emphasizes these latter points.

DIAGNOSIS (emended). Deep-bodied fish similar to *Cleithrolepidina*, but in which the skull is extremely deep. The maxilla tapers slightly anteriorly, but is deep throughout its length. A large triangular premaxilla present. Snout extremely deep so that the nasal is roughly 4·5 times as deep as it is long. Postrostral as long as the frontal. Extrascapular divided into four elements.

TYPE (and only certain) SPECIES. *Cleithrolepis granulata* Egerton.

In 1941 Wade compared *Cleithrolepis granulata* with *Cleithrolepis* (now *Cleithrolepidina*) *minor* (Wade 1941b : 391–2). It is important to examine the differences which he thought existed between these two forms because he concluded that the two were quite distinct. Wade did not attempt to separate *C. granulata* and *C. minor* into separate genera, even though he concluded that, whereas *C. minor* was a typical perleidid, *C. granulata* was quite distinct from that family. The differences noted by Wade will now be listed and examined.

1. The dorsally angulated body of *C. minor* has become more gently curved in *C. granulata*.

This difference, although present, is very slight and would not seem to warrant distinction between the two forms at anything above the species level, being of the same order as variation of skull length relative to that of the body.

2. The temporal region of *C. minor* is shallow, and that of *C. granulata* is deep.
3. The simple tabulars of *C. minor* are divided in *C. granulata*.

Both these differences are certainly present but cannot be regarded as having great significance as they can be simply related to the acquisition of a deeper skull in *C. granulata*.

4. In *C. granulata* (but not in *C. extoni* or *C. minor*) there is a second preoperculum bearing a preopercular sensory canal.

The second preoperculum referred to by Wade is here called a quadratojugal (see Westoll 1944 : 73). This bone has been identified in both *C. minor* and *C. extoni* as well as *C. granulata*. Wade's suggestion that there was a functional relationship between the presence of a second preoperculum (quadratojugal) and the development of a preopercular peg or process which articulated with the maxilla may well be correct. In *C. extoni*, which has a relatively small quadratojugal, the preopercular process is short and is not overlapped by the maxilla. The presence of a quadratojugal and a preopercular process in *C. minor*, *C. extoni* and *C. granulata* serves to unite rather than to separate the three species.

5. There are few branchiostegals in *C. minor* but about a dozen in *C. granulata*. Branchiostegals are reduced in most perleidiforms; the presence of a large number in *C. granulata* may show that the genus did not evolve directly from *C. minor*, but it certainly does not imply that the two taxa should be placed in separate families.

6. The circumorbital bones are well developed in *C. granulata* and narrow in *C. minor*.

This difference in fact applies only to the supraorbital bones, and even these are not as narrow in *C. minor* as Brough's reconstruction suggests. In *C. extoni* the supraorbitals are even deeper than in *C. granulata*.

7. The suture between the maxilla and the preopercular in *C. minor* runs diagonally across the cheek to a point behind the orbit. In *C. granulata* this suture runs to a point below the orbit.

This difference is valid, but its taxonomic importance is lessened by the fact that *C. extoni* displays an intermediate condition in this respect.

In conclusion, the differences between *C. minor* and *C. granulata* noted by Wade do not indicate that the two forms have affinities with different families. Many characteristics of *C. granulata* such as the divided extrascapular and the deep dermopterotic can be related to the fact that in *C. granulata* the skull in general and the maxilla in particular are unusually deep. These differences serve to separate *Cleithrolepidina minor* and *Cleithrolepidina extoni* from *Cleithrolepis granulata* and to justify separation at the generic level only. The genera *Cleithrolepis* and *Cleithrolepidina*, however, share some very unusual features and must be regarded as members of one family (see discussion on the classification of the Perleidiformes, p. 335).

Cleithrolepis granulata Egerton
(Figs 43–44)

1864 *Cleithrolepis granulatus* Egerton: 3, pl. 1.
1890 *Cleithrolepis granulatus* Egerton; Woodward: 39–42, text-fig., pl. 7, figs 1–7, pl. 8, figs 2–3.
1895 *Cleithrolepis granulatus* Egerton; Woodward: 155–156.
1908 *Cleithrolepis granulatus* Egerton; Woodward: 25.
1935 *Cleithrolepis granulata* Egerton; Wade: 49–57. text-figs 22–26, pl. 6, fig. 3.

HORIZONS AND LOCALITIES. Triassic of Cockatoo Island, near Sydney, N.S.W.; Scythian or Anisian Narrabeen shales at Gosford, N.S.W.; Ladinian (?) Hawkesbury Sandstone at Beacon Hill, Brookvale, N.S.W.; and Wianamatta shales at St. Peters, N.S.W.

DIAGNOSIS (emended). Parietal equidimensional with convexo-concave ventral edge. Dermopterotic deep posteriorly. Opercular with slightly convex ventral edge. Thirteen branchiostegal rays and gular plate present. Preopercular constricted dorsally between a dermohyal and a suborbital, with an anterior process overlapped by postero-dorsal border of maxilla. Posterior supraorbital equidimensional. Small teeth present at anterior tip of lower jaw.

Supracleithrum in contact dorsally with accessory dermopterotic and with extrascapular.

HOLOTYPE. A specimen in the Australian Museum; see Egerton 1864 : pl. 1, fig. 3.

MATERIAL. P.15752 and counterpart P.15753, P.15754–6, P.15759, P.15761, P.15766–70, P.15773, P.24674, P. 24675.

G.N. 419, 422 and counterpart 438.

U.S.G.D. 91, 167, 217, 203 (at the University Museum of Zoology, Cambridge).

All the specimens studied were from the Brookvale locality.

DESCRIPTION. The species has been described in detail by Wade (1935 : 49–57) and a full description will not be repeated here. However, there are several differences between Wade's restoration of the species and that given here, and these are noted in the description below.

Size (Fig. 43). The body shape is similar to that of *Cleithrolepidina extoni* (see Fig. 40); however, the head, as noted by Wade, is significantly larger than in *C. extoni*.

Skull (Fig. 44). The frontal is long and somewhat deeper than in *C. extoni*. The supraorbital sensory canal does not appear to extend onto the parietal. Posterior to the parietal, the extrascapular is divided into four elements which become

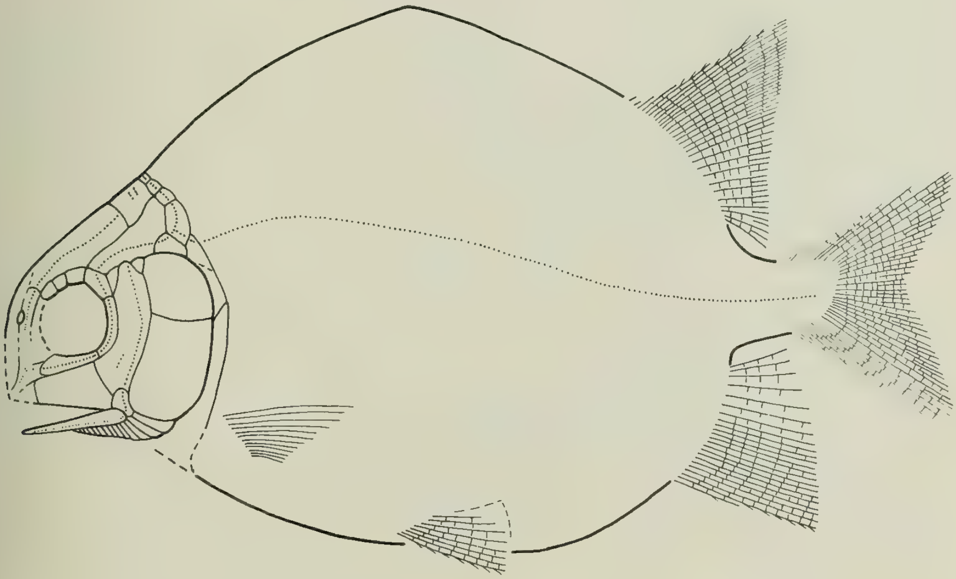

FIG. 43. *Cleithrolepis granulata* Egerton. Restoration, ×1·5 approx. Scales omitted.

progressively larger ventrally. The dermopterotic is similar in shape to that in *C. extoni*, except that it is deeper, especially posteriorly. The infraorbital sensory canal runs roughly through the centre of the dermopterotic, and is not limited to the ventral edge of this bone. There is no sign of subdivision of the dermopterotic as figured by Wade (1935 : text-fig. 23); however, there is a lozenge-shaped element lying between the ventral edge of the extrascapular and the dorsal edge of the opercular (P.15754). Comparison with *C. extoni* suggests that this bone is an accessory dermopterotic.

The opercular series is inclined antero-ventrally at an angle similar to that seen in *C. extoni*. The opercular is 'D'-shaped, and there is a triangular dermohyal at its

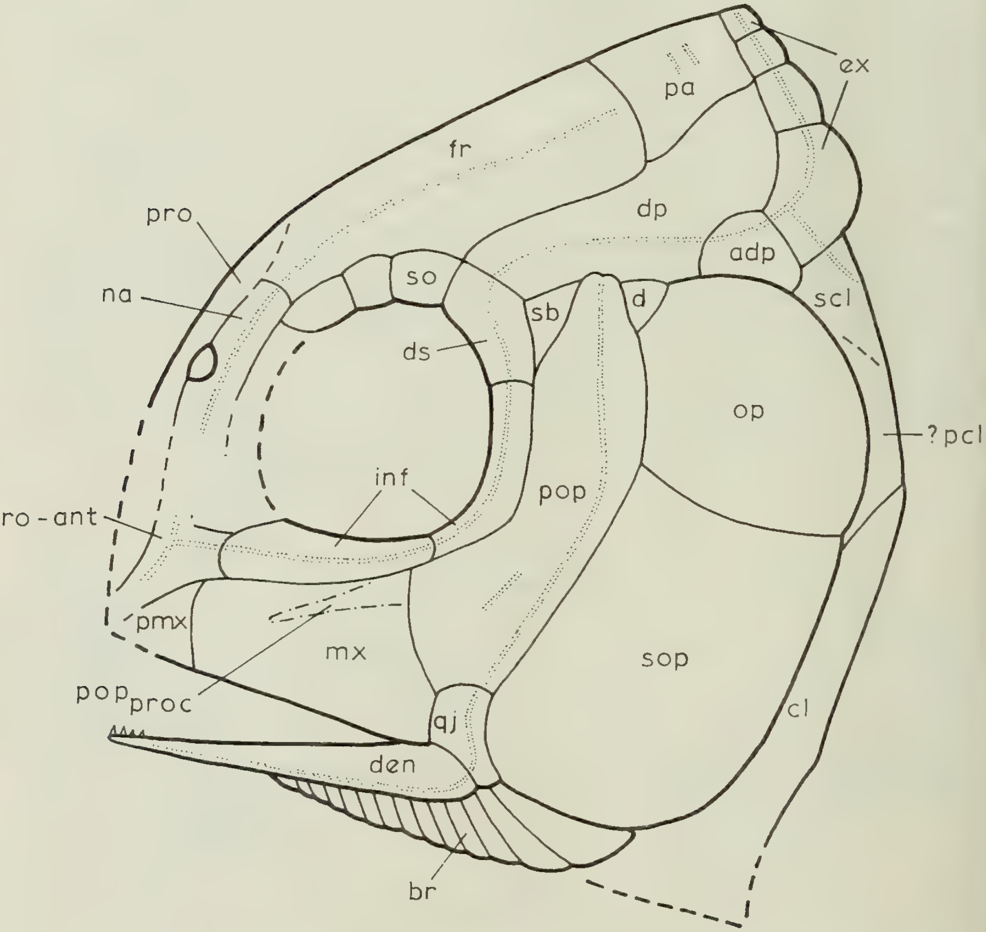

FIG. 44. *Cleithrolepis granulata* Egerton. Restoration of skull and pectoral girdle, ×4·5 approx.

antero-dorsal corner (G.N. 419). The subopercular is deeper than that of *C. extoni*, and is roughly rectangular in shape, being wide ventrally.

The preopercular differs from that of *C. extoni* in that its depth is greater and its ventral part extends further anteriorly, so that the suture between it and the maxilla lies almost below the centre of the orbit. Also, the antero-ventral process of the preopercular does not extend between the maxilla and infraorbitals as is the case in *C. extoni*, but is completely overlapped by the maxilla so that it is not visible in lateral view (G.N. 419, Fig. 43). At the ventral end of the preopercular there is a quadratojugal.

The maxilla is quite different from that of *C. extoni* in that it is deep throughout its length.

Three supraorbital elements border the dorsal part of the orbit (G.N. 419). The anterior of these elements does not appear to extend ventrally to border the anterior part of the orbit, although Wade (1935 : 51) has noted the occurrence of such an element in a single specimen, U.S.G.D. 135 (this specimen was not available for study).

The snout of *C. granulata* appears to be similar to that of *C. extoni* except that the nasal and postrostral elements are considerably elongated, the skull being much higher at this point. There is a premaxilla at the ventral tip of the snout. A rostral is not preserved, and it is possible that there has not been any fragmentation of the rostro-antorbital (see Gardiner 1963 : 312).

The lower jaw is straight and extremely slender. In specimens P.13953 and P.24675 three or four tiny teeth are preserved at the extreme tip of the lower jaw.

Pectoral girdle. There is no suprascapular. Dorsal to the cleithrum an element extends to meet the bone identified as an accessory dermopterotic. There are faint indications in specimen P.15761 that this element is subdivided by an oblique suture, and that a postcleithrum therefore separates the cleithrum from an extremely small supracleithrum. The dorsal end of the supracleithrum is in close contact both with the accessory dermopterotic and with the ventral extrascapular element.

Paired fins. The pectoral fin contains 12 rays. No bifurcation, jointing or fringing fulcra are preserved. The pelvic fin contains at least 8 rays which have up to 8 joints. The anterior ray bears fringing fulcra.

Unpaired fins. All the unpaired fin-rays are jointed and the anterior rays bear fringing fulcra. The posterior rays of the dorsal and anal fins are widely spaced. The dorsal fin contains 26 rays which have between 3 and 10 joints. All the rays bifurcate distally. The anal fin contains 24 rays which have between 3 and 9 joints, but no bifurcation was observed. The caudal fin contains a total of 37 rays, 12 of which are epaxial in position. The rays have up to 10 joints and are bifurcated.

Squamation. There are 40 body transverse scale rows. The morphology of the scales is very similar to that of *C. extoni* and they bear an ornament of numerous tubercles.

A description of the axial skeleton, and of variation of morphological details during development in *C. granulata*, has been given by Wade (1935 : 53–56).

Family **HYDROPESSIDAE** nov.

Diagnosis. As for the genus *Hydropessum.*

Genus ***HYDROPESSUM*** Broom 1909

1909 *Hydropessum* Broom: 266.

Diagnosis (emended). Head deep posteriorly. Bones of the skull roof ornamented with tubercles, those of the opercular series with rugae. Parietal short and deep. Frontal extremely deep. No accessory dermopterotic present. Opercular series forming a 'D'-shaped plate. The suture dividing the opercular and subopercular oblique, so that the anterior margin of the subopercular is shorter than that of the opercular and the posterior margin of the opercular is shorter than that of the subopercular. The ventral border of the subopercular is concave. No dermohyal present. About seven branchiostegals present. Preopercular without anteroventral process seen in *Cleithrolepis.* Ventral end of preopercular broad, and extending anteriorly to a point almost level with the midpoint of the orbit. A large element, probably an accessory preopercular, extending dorsally over halfway along anterior edge of subopercular, and anteriorly almost halfway along upper jaw margin. Only anterior part of upper jaw margin formed by maxilla. Infraorbitals narrow. Two supraorbitals present. Nasal bordering anterior margin of the orbit. Snout consisting of paired nasals separated by a postrostral and, probably, paired rostro-antorbitals and paired premaxillae. Lower jaw short and stout. Teeth probably absent.

Body deep, diamond-shaped with corners at the head and tail, and midway along the dorsal and ventral sides. Maximum body depth equal to length from snout tip to end of caudal lobe. Suprascapular large and 'D'-shaped. Scales deep and ornamented with elongate rugae. Scales in pectoral region orientated parallel to those on the rest of body. Dorsal and anal fins situated with their anterior rays inserted at the deepest part of the body. Pelvic fins probably lost.

Type (and only) species. *Hydropessum kannemeyeri* Broom.

Remarks. The genus *Hydropessum* was previously included in the Cleithrolepididae (Wade 1935, Berg 1940, Gardiner 1967).

Hydropessum kannemeyeri Broom
(Figs 45–47)

1909 *Hydropessum kannemeyeri* Broom: 266–267, pl. 12, fig. 5.

Horizon and locality. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis. As for the genus *Hydropessum.*

Holotype. S.A.M. 1334.

Material. P.16042, P.16180 and counterpart P.16181. G.N. 358.

Description. *Size* (Fig. 45). The total length of the best preserved specimen, P.16180, is estimated to have been about 95 mm. It is 77 mm at its greatest depth. The body is diamond-shaped.

Skull (Fig. 46). The bones of the skull roof are ornamented with tubercles, and those of the cheek and opercular regions with rugae.

The frontal is an extremely broad bone having its widest point about midway along its length (P.16181, Fig. 47). The opercular and subopercular are extremely

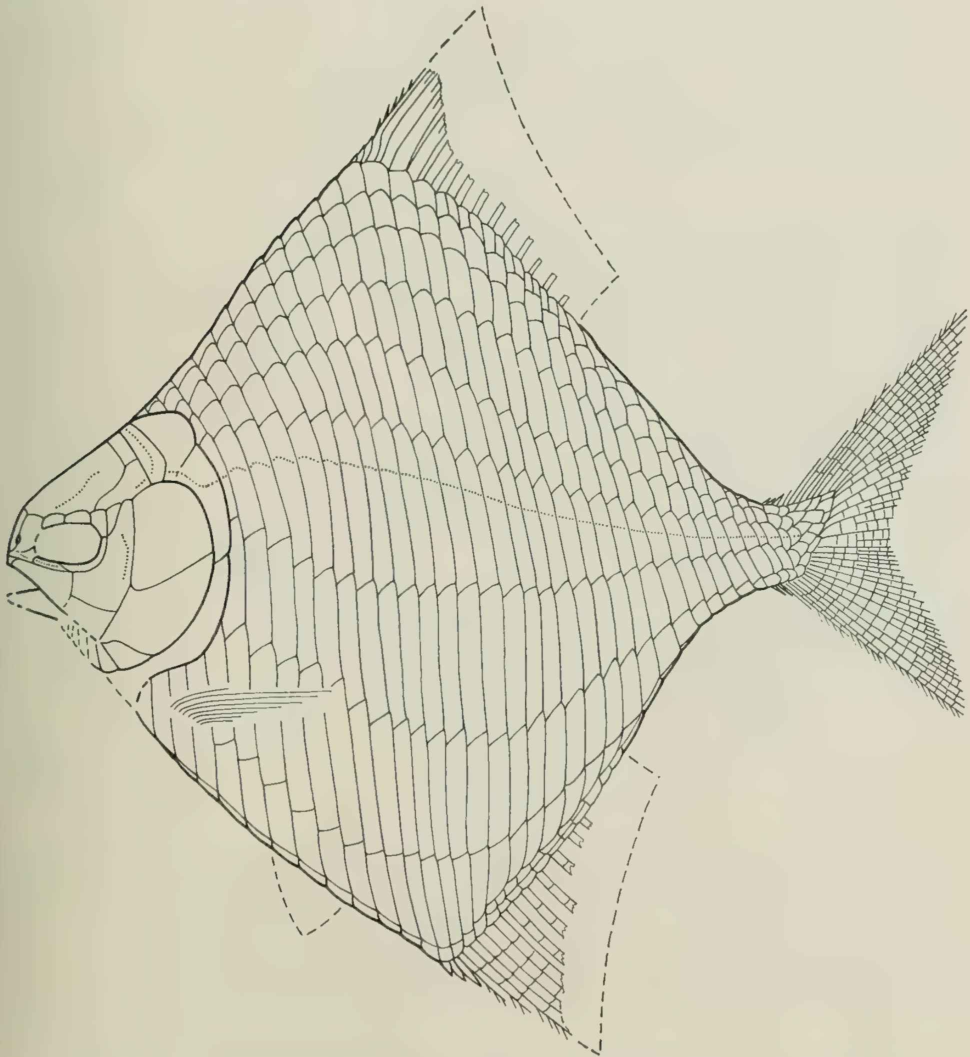

Fig. 45. *Hydropessum kannemeyeri* Broom. Restoration. ×1·5 approx.

large. Together they form a 'D'-shaped plate which extends to a point well below the level of the snout tip. In consequence, the upper jaw margin slopes antero-dorsally from the antero-ventral corner of the subopercular. The angle between the anterior edge of the opercular series and the ventral edge of the maxilla is 62°. On the medial surface of the antero-dorsal corner of the opercular there is a deep notch which received the opercular process of the hyomandibular (G.N. 358). The opercular is ornamented with elongate rugae which radiate from its antero-dorsal

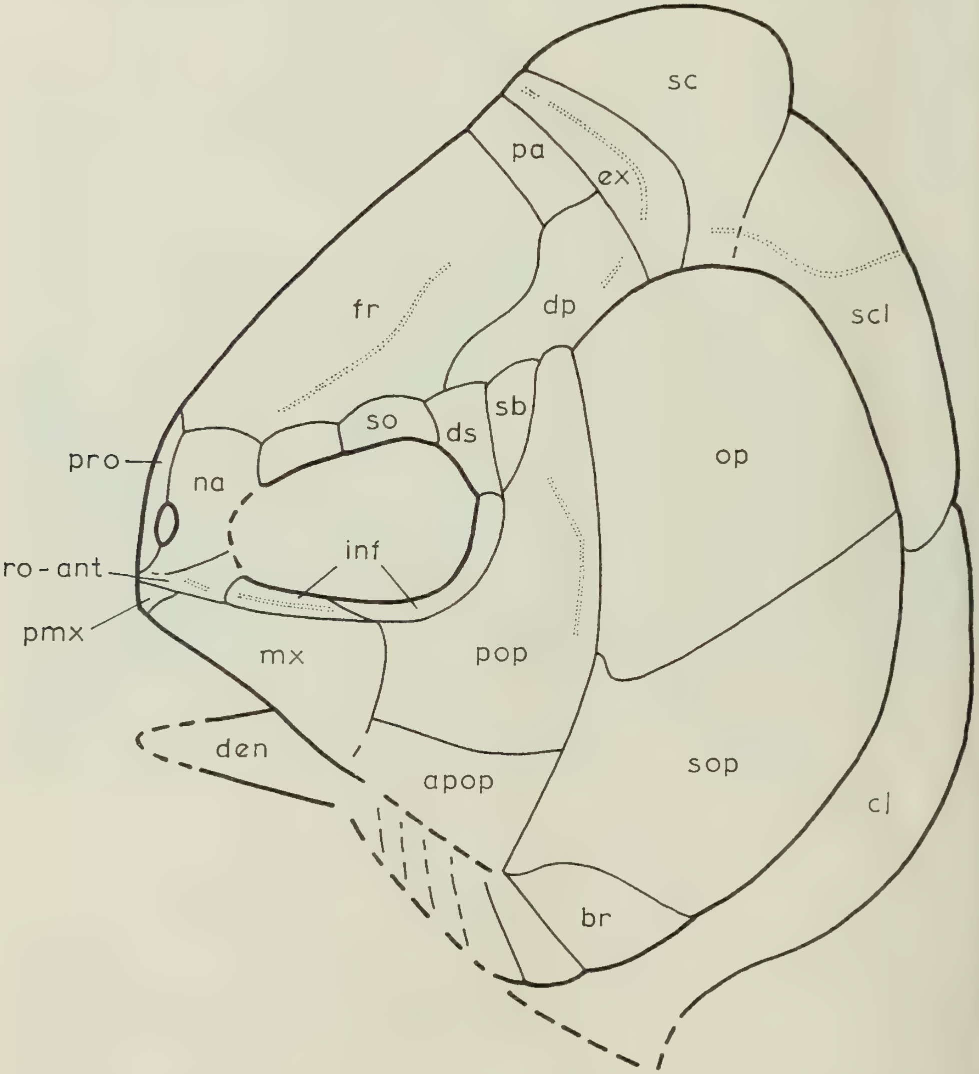

FIG. 46. *Hydropessum kannemeyeri* Broom. Restoration of skull and pectoral girdle, ×5·5 approx.

corner and the subopercular with rugae which radiate from its antero-ventral corner. Six or seven branchiostegal rays are present.

The preopercular is 'L'-shaped. Its dorsal part is narrow and constricted anteriorly by a single triangular suborbital. The preopercular sensory canal does not extend to the dorsal tip of the preopercular, but turns antero-dorsally at a level just below that of the centre of the opercular. There is no dermohyal. The lower part of the preopercular is deep. It extends anteriorly so that the vertical suture between it and the maxilla lies below the centre of the orbit. The ventral part of the preopercular is separated from the upper jaw margin by a rectangular bone which sutures anteriorly with the maxilla, dorsally with the preopercular and posteriorly with the subopercular. This bone is clearly not a fragment of the maxilla because it bears fine striae which, in some cases, run at right angles to those on the maxilla (P.16181, Fig. 47). The identity of this bone is uncertain, there being no obvious way of deciding whether it is a quadratojugal or a separate preopercular element. There are no traces of the preopercular sensory canal on this bone. Tentatively this bone will be called an accessory preopercular.

The maxilla is wedge-shaped and very short, so that it contributes to only half of the upper jaw margin. At its tip there is a small premaxillary element (P.16180). No teeth were observed. The dorsal part of the snout is composed of a median postrostral which separates the broad nasals. The nasal probably borders the anterior edge of the orbit. The snout is completed by a wedge-shaped rostro-antorbital.

The lower jaw is only partially preserved (P.16181, Fig. 47). It is deep and tapers anteriorly. When restored to match the length of the upper jaw, it appears to have been a short, rather heavy structure. No dentary teeth were observed.

Pectoral girdle. All the pectoral elements are ornamented with elongate sinuous rugae. The suprascapular lies immediately behind the extrascapular, and is 'D'-shaped and extremely large.

The supracleithrum is broad and its rounded ventral end extends below the level of the posterior part of the suture between the opercular and subopercular. There are faint traces of a suture between the cleithrum and a clavicle (P.16180).

Paired fins. The pectoral fin is poorly preserved in specimen G.N. 358 where it has at least 8 rays, but no other details can be seen.

There is no trace of the pelvic fin in any specimen, and it seems likely that it is not present (c.f. *Bobasatrania* and *Amphicentrum*).

Unpaired fins. The anterior rays of both the dorsal and anal fins arise at the deepest part of the body. Only the proximal ends of the rays in both cases are preserved and the exact shape of these fins is therefore unknown. In both fins, however, the anterior rays bear fringing fulcra and are closely spaced and become increasingly widely separated posteriorly. No jointing was observed in the dorsal fin-rays but there were indications of bifurcation. In the anal fin jointing is definitely present, but no bifurcation was seen. It is likely that the rays were jointed and bifurcating in both fins.

The caudal fin is borne on a short body lobe. There are 30 rays, 10 of which are epaxial in position. The anterior rays of both the dorsal and ventral lobe are closely spaced, bear fringing fulcra and are long. The tail has a high aspect ratio. All the caudal fin-rays are bifurcated, the longest rays twice.

Squamation. There are 34 body transverse scale rows. There is no reversal of the scale rows below the pectoral fin as is seen in *Cleithrolepis*. The scales are deepest in the lateral line region where the depth of some is almost 10 times their length this ratio takes into account only that part of the scale which is not overlapped by adjoining scales). The scales close to the dorsal and ventral edges of the body

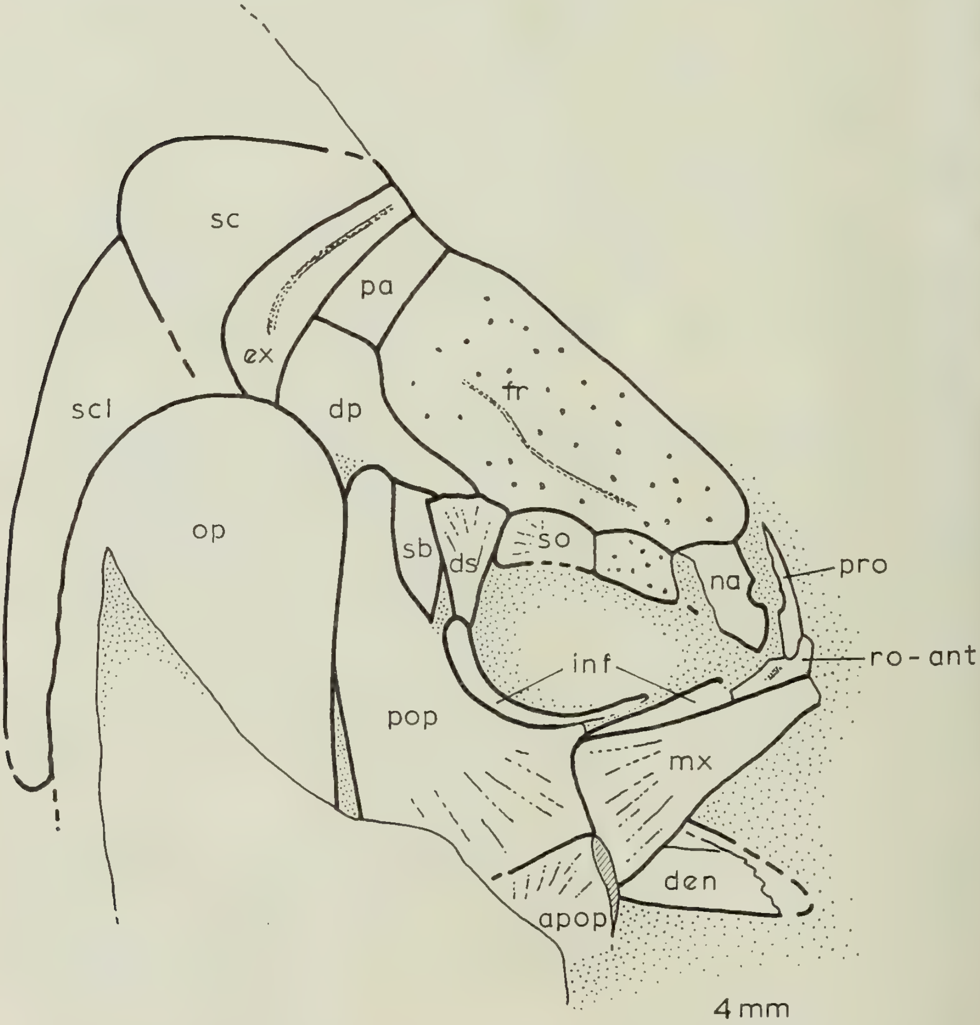

FIG. 47. *Hydropessum kannemeyeri* Broom. P.16181: impression of left side.

are almost equidimensional, those close to the base of the anal fin being particularly small. The flank scales bear an ornament of long rugae, while those at the dorsal and ventral edges of the body have short sinuous rugae.

GENERA PROVISIONALLY ASCRIBED TO PERLEIDIFORMES

Cleithrolepis cuyana Bordas

1944 *Cleithrolepis cuyana* Bordas: 457–458, pl. 2.

HORIZON AND LOCALITY. Triassic. Bituminous rocks, Santa Clara, Mendoza and San Juan provinces, Argentina.

REMARKS. This form is deep-bodied and has a skull with a blunt snout and large orbits. The bones of the skull, however, have not been preserved well enough to allow any description. Thus the inclusion of this form in the genus *Cleithrolepis*, or even the order Perleidiformes, remains provisional.

Dipteronotus cyphus Egerton

1854 *Dipteronotus cyphus* Egerton: 369–371, pl. 11, figs 1–2.
1910 *Dipteronotus cyphus* Egerton; Woodward: 322–323.

HORIZON AND LOCALITY. Lower Keuper, Bromsgrove, Worcestershire.

HOLOTYPE. G.S.M. 18188 and counterpart 18189, the only specimen known.

REMARKS. The body shape of *D. cyphus* is extremely similar to that of *Cleithrolepis* and *Cleithrolepidina* in that there is a dorsal 'hump' occurring almost halfway along the body. The dorsal and anal fins lie posterior to the deepest part of the body, but do not appear to extend as close to the caudal fin as they do in *Cleithrolepis* and *Cleithrolepidina*. The anterior dorsal fin identified by Egerton (1854 : 370) in fact consists of a group of displaced body scales. Little of the skull anatomy can be determined except that the orbit is large and anteriorly placed, and the opercular series orientated vertically. The scales do not bear any ornament and are deep, but not as deep as in known cleithrolepids.

III. DISCUSSION

(a) Classification of the Redfieldiiformes.

(i) *Brookvaliidae and Redfieldiidae.*

The differences between the families Brookvaliidae and Redfieldiidae are as follows:

	Brookvaliidae	Redfieldiidae
1.	Orbit large.	Orbit small.
2.	Dermosphenotic narrow and crescent-shaped, tapering to a point anteriorly.	Dermosphenotic deep and roughly rectangular.

3. Infraorbitals narrow, reduced in some genera.	Infraorbitals never reduced.
4. Antorbital excluded from snout margin by toothed element (probably a premaxilla).	Antorbital bordering ventral margin of snout. No premaxilla.
5. Adnasal absent or small, having, at most, point contact with dermosphenotic.	Adnasal large with broad contact with dermosphenotic.
6. Four parietals (except *Atopocephala* which has two).	Two parietals (except *Helichthys* which has four, and *Redfieldius* which has three or four).
7. Posterior part of supraorbital sensory canal, if present, on dermopterotic.	Posterior part of supraorbital sensory canal, if present, on parietal.
8. Antopercular present.	No antopercular (except in two species of *Helichthys*).
9. Lower jaw slender, long and curved dorsally towards the symphysis.	Lower jaw deep, short, and either straight or curved dorsally towards the symphysis.

In order to compare the orbit size in the various redfieldiiform genera, measurements were taken from restorations in this study, from Schaeffer (1967) and in one case (*Dictyopyge decipiens*) from Brough (1931). A vertical line was drawn which passed halfway between the anterior and posterior edges of the orbit. The height of the orbit, and of the head, was measured along this line and the ratios between these two measurements calculated (Table 1).

Table 1

The relative orbit size in redfieldiiform genera.

Genus	Vertical height of orbit in mm A	Vertical height of skull in mm B	A / B
Brookvaliidae			
Ischnolepis	51·5	69	0·75
Atopocephala	38	52	0·73
Brookvalia	43	59·5	0·72
Phlyctaenichthys	43	60·5	0·71
Redfieldiidae			
Daedalichthys	45	73	0·62
Helichthys	31	58	0·53
Geitonichthys	34·5	71·5	0·48
Molybdichthys	42·5	78	0·54
Dictyopyge (*decipiens*)	14	34	0·41
Cionichthys	20·5	34·5	0·59
Redfieldius	18·5	34	0·54
Lasalichthys	20	35·5	0·56
Synorichthys	20·5	36·5	0·56

The value of this data by itself might be regarded as slight, but significantly, the relative orbital sizes can be correlated with the shape of the dermosphenotic. In the brookvaliids this element is curved and narrow, tapering to a point anteriorly, whereas in redfieldiids it is deep and rectangular except that its ventral edge is excavated where it borders the orbit.

The snout of the North American redfieldiids is now well known (Schaeffer 1967). The antorbital is a large element bordering the anterior edge of the orbit, the ventral edge of the snout and the ventral edge of the nostril. There is a large adnasal between the dorsal part of the antorbital and the anterior end of the dermosphenotic. The dorsal part of the nostril is bordered by a narrow nasal, and the postrostral may or may not be present. The snout tip is capped by a rostral and there is no premaxilla.

The Lower Triassic African redfieldiids, *Daedalichthys* and *Helichthys*, have an identical snout pattern to that just described. The Middle Triassic Australian genera, *Geitonichthys* and *Molybdichthys* are also very similar, differing only in the shape of the antorbital which is rectangular and extends so far anteriorly that it borders the anterior as well as the posterior edge of the nostril. Participation of the antorbital in the infraorbital bar is limited.

The snout of brookvaliids is rarely well preserved, but enough of its structure is now known to suggest important differences between the two families. In the Brookvaliidae, a toothed element excludes the antorbital from the ventral margin of the snout. The antorbital is a narrow crescent-shaped element bordering the anterior edge of the orbit. Its anterior part is limited to a narrow projection which borders the ventral edge of the nostril, and which carries the ethmoid commissure. The adnasal is either a small diamond-shaped element having point contact or no contact with the dermosphenotic (*Brookvalia*), or is lacking altogether (*Ischnolepis* and probably *Atopocephala* and *Phlyctaenichthys*).

The cheek region in both families is variable but differences can be related to the evolution of a more upright suspensorium, a trend which occurred independently in various genera.

(ii) *Schizurichthyidae.*

Schizurichthys is known by a single species, *S. pulcher*, which is incompletely preserved, but which has several characteristics unique among the Redfieldiiformes. It obviously represents a group quite isolated from other known members of the order, and therefore a new family, Schizurichthyidae, is proposed to include the genus.

The unique characters of the Schizurichthyidae are seen in the configuration of the snout elements, the length of the lower jaw and the structure of the caudal fin and scales.

The dermosphenotic is similar to that of the Brookvaliidae in that it is crescent-shaped and comes to a point anteriorly. The antorbital borders the anterior edge of the orbit, but is excluded from the ventral edge of the snout by a toothed element. Unlike the Brookvaliidae, however, the antorbital is deep ventrally, so that its shape resembles that of an inverted hatchet. The profile of the snout as a whole differs from that of both the Brookvaliidae and Redfieldiidae in that the upper jaw runs smoothly to the snout tip, and is not sharply upturned just below the orbit.

The lower jaw is moderately deep and curves dorsally towards the symphysis. It is unique in that it extends to the level of, or even beyond, the snout tip.

The tail has a structure unknown in any redfieldiiform, and is probably unlike that of any known actinopterygian. The 6 anterior rays of the upper caudal fin lobe originate on the dorsal side of the body lobe. The first and sixth rays bear fringing fulcra. The seventh ray, which originates at the tip of the body lobe, also bears fringing fulcra (Fig. 28).

The scales of brookvaliids and redfieldiids vary in shape from rhombic to leaf-shaped. They are smooth, or bear ornament consisting of one to four elongate rugae. In *Ischnolepis* the rugae are seen to consist of single rows of closely associated tubercles. The posterior margins of the scales of *Daedalichthys* are denticulated, but their overall shapes is still rhombic. The scales of *Schizurichthys* vary in shape from subcircular to rectangular (Fig. 30). They bear pronounced pegs on their dorsal edges and sockets on their ventral edges, and they are ornamented with rows of tubercles which radiate from a point close to the antero-dorsal corner of the scale. In these three characteristics, the scales of *Schizurichthys* are unique within the Redfieldiiformes.

(iii) *Redfieldiiformes—discussion*

Orbit and dermosphenotic. Brough (1936 : 400) has suggested that during the evolution of the Redfieldiiformes (his Catopteridae) the orbit became smaller. This view is difficult to substantiate. In the first instance, the series showing supposed reduction of the orbit (Brough 1936 : text-fig. 10) is not arranged in strict stratigraphic order; secondly, genera considered here to belong to separate families were then discussed together. The fact that redfieldiids, which have small orbits, were more abundant than brookvaliids during the Upper Triassic, gave apparent support to the incorrect hypothesis that there was an evolutionary trend in the Redfieldiiformes towards a decrease in orbit size. There is, in fact, little evidence of any change in orbit size in either the redfieldiids or the brookvaliids: *Helichthys* has an orbit comparable with those of Upper Triassic redfieldiids, and the earliest known brookvaliid, *Ischnolepis,* has an orbit very similar to that of *Brookvalia.*

Schaeffer (1967 : 331) is of the opinion that the narrowness of the dermosphenotic in *Atopocephala* is related to the large size of the orbit, but in *Brookvalia* to posterior expansion of the frontal. The second interpretation was necessary because in Wade's figure of *Brookvalia* (1935 : text-fig. 5) the vertical height of the orbit is underestimated. In fact, the orbit in *Brookvalia* is large, and there seems to be no reason to suppose that the narrowness of the dermosphenotic is related to any factor other than the large orbit.

Infraorbitals. Brough (1936 : 401) remarks that loss of infraorbitals (his suborbital bones) constitutes 'one of the clearest trends to be observed in the family'. In view of his opinion that another trend was towards reduction of orbital size, this opinion seems, on theoretical grounds, surprising. Once again, there is no evidence of any particular evolutionary trend with regard to the infraorbitals. What is apparent is that the infraorbitals are narrow or reduced in the brookvaliids, and slightly broader in redfieldiids. This slight difference is almost certainly related to the difference in orbital size between the two families.

Cheek region. In refuting Brough's opinion (1936 : 390) that there was a trend within the Redfieldiiformes from oblique to vertical orientation of the suspensorium, Schaeffer (1967 : 335) states that, with the exception of *Brookvalia*, there is little change in this character from early to late Triassic times. I cannot agree with this latter opinion. The angle between the anterior edge of the subopercular and the ventral region of the maxilla (an angle more easily measured than the true angle of the suspensorium, and certainly related to it) varies as much as 10° within the families Brookvaliidae and Redfieldiidae (cf., for example, *Ischnolepis* with *Phlyctaenichthys*, and *Geitonichthys* with *Cionichthys*). As few of the known redfieldiiform genera are closely related to one another, this variation implies that the angle of the suspensorium was becoming steeper in several phylogenetic lines within the order.

Pectoral girdle and fins. Watson (1925 : 824) has shown that the palaeoniscoid pectoral fin is primitively broad based with an insertion which runs parallel to the body axis. In later palaeoniscoids the base of the pectoral fin became narrower (White 1939 : text-fig. 12) and its orientation relative to the rest of the body also changed. Westoll (1944 : 83) has shown that the base of the pectoral fin in haplolepids, and probably in most palaeoniscoids, is inserted so that the anterior end of the fin base is slightly raised. The functional explanation for this orientation is that in this position the pectoral fin acts as a hydrofoil providing lift at a point anterior to the centre of gravity of the fish; this counteracts the lift created by the swimming movement of a heterocercal tail.

In *Ischnolepis* the pectoral fin appears to be inserted on a vertical margo radialis, and it is possible that the pectoral fin in the other Redfieldiiformes was similarly orientated.

The function of a vertically orientated pectoral fin is to act as a brake, a function found almost exclusively in teleosts. If the pectoral fin of Redfieldiiformes functioned in a similar way it would appear to have lost its original hydrodynamic function. One of the most distinctive characteristics of Redfieldiiformes (exclusive of the Schizurichthyidae) is the upturned snout. This snout is probably an adaptation to special feeding habits, but it quite possibly could have performed a secondary, hydrodynamic function, and allowed other selective pressures to influence the orientation of the pectoral fin.

When a fin acts as a brake rather than as a hydrofoil, it is subjected to direct water pressure, and so must be fairly rigid. The pectoral fins of Redfieldiiformes (and to a lesser extent the pelvic fins) are remarkable in that their structure is modified to a considerably greater extent than is the structure of the other fins (Brough 1936 : 391). The rays have few joints or are unjointed, and are stout compared with other fin-rays.

(b) A functional analysis of the redfieldiiform skull.

The redfieldiiform skull resembles that of most other palaeoniscoids in that the maxilla is firmly fused to the preopercular and to the infraorbital bones. The orientation of the suspensorium varies from oblique to vertical. There are, however, several anatomical features which indicate that the Redfieldiidae, at least, had a specialized feeding mechanism. That this mechanism was efficient is indicated by the ubiquity of the family at a time when forms with the holostean feeding mechanism were rapidly replacing the more primitive palaeoniscoids.

Two important functions of the fish skull are, firstly, to provide a flow of water over the gills, and secondly, to contain an efficient feeding mechanism. These will now be discussed in turn with reference to the Redfieldiiformes.

(i) *Gill ventilation.*

Hughes and Shelton (1958) have emphasized that gill ventilation depends upon the operation of two pumps; the buccal cavity which, when adducted, acts as a force pump; and the opercular cavities which, on abduction of the operculars, act as suction pumps. Abduction of the operculars closely follows adduction of the buccal cavity so that a more or less continuous flow of water overcomes the resistance of the gill. Moreover, 'Depending upon the relative size of the cavities and on the extent of their volume change, it is possible for either the buccal pressure pump or the opercular suction pump to become the dominant ventilating mechanism in different species' (Hughes & Shelton 1958 : 822).

There are three indications that the redfieldiiform opercular pump was weak. In most genera the opercular series is remarkably narrow, in consequence the underlying opercular cavity could not have been very large. Also the presence of only one branchiostegal ray must, as noted by Schaeffer (1967), have restricted the opercular opening to the side of the head. Thirdly, evidence from *Ischnolepis* and *Brookvalia* shows that the hyomandibular did not articulate with the opercular at a point close to the latter's antero-dorsal corner. As a result, contraction of the dilator operculi could only have had a limited effect on the opercular, and it seems likely that abduction of the opercular was neither extensive nor powerfully executed. If the opercular pump was weak, it follows that the buccal pump was correspondingly powerful, for there is no reason to suppose that the Redfieldiiformes could ventilate their gills by continuous swimming as do some teleosts. A result of having a powerful buccal pump is that an unusual feeding mechanism in the Redfieldiidae was made possible.

(ii) *Feeding*

The main differences between the three redfieldiiform families appear to be broadly related to different methods of feeding. *Schizurichthys* is similar to many palaeoniscoids in which the upper and lower jaw tooth rows are long, with the lower jaw extending to a point level with the tip of the snout, and in which the suspensorium is oblique. These characters indicate that *Schizurichthys* was probably a predator in which feeding consisted of simply seizing food in the jaw and swallowing small prey whole, or biting pieces off a larger mass.

The brookvaliids show few departures from this method of feeding, and were probably quite versatile in their habits. The fact that the lower jaw is slightly shorter than the upper jaw indicates that these genera probably fed on the bottom for at least some of the time, and stomach contents in *Brookvalia gracilis* which appear to consist of small molluscs (P.15847, P.15848, P.17013, P.24711 and P.24712) support this hypothesis.

The redfieldiids were also bottom feeders, and Schaeffer (1967) has suggested that they scooped detritus from the river or lake bottom. Whilst agreeing in general with this hypothesis, I believe there is good evidence that the redfieldiids were active suction feeders.

In teleosts the buccal cavity is an effective suction pump not only because it is capable of extreme expansion, but also because this expansion is supplemented by the upper and lower jaws which can be thrust anteriorly to form a protrusible tube. Such a mechanism is not possible in redfieldiids because the gape of the jaws is long, and abduction of the lower jaw would cause immediate loss of negative pressure created by abduction of the branchial basket. However, it is quite likely that considerable negative pressure in the buccal cavity could be achieved by independent abduction of the branchial basket. In this connection it should be noted that in all redfieldiid genera, the lower jaw is consistently shorter than the upper jaw. The length of the lower jaw cannot be correlated with forward shift of the jaw articulation for, even in a genus such as *Daedalichthys* which has an oblique suspensorium, the tip of the lower jaw falls well short of the level of the snout tip. In consequence the redfieldiid buccal cavity may have opened ventrally through a crescent-shaped gap, even when the jaws were closed.

The mechanism by which the branchial basket is abducted in actinopterygians has been described by Schaeffer and Rosen (1961). First the ventral part of the pectoral girdle is pulled postero-ventrally by the ventro-lateral muscles inserted on the cleithrum, then the anterior part of the copula and of the hyoid bar is pulled postero-ventrally by the sternohyoid muscle which extends from the cleithrum to the hyoid bar. If, as I suggest, such expansion of the buccal cavity in the Redfieldiidae was capable of producing a suction powerful enough to be used as a feeding device, one would expect the development of an unusually extensive ventro-lateral and sternohyoid musculature. Such development would be reflected by the size of the copula and of the ventral part of the pectoral girdle. Unfortunately, copulae are not preserved in any redfieldiid, but comparison with the Brookvaliidae shows that the cleithrum in the Redfieldiidae is an exceedingly large and robust element.

As well as the muscles described above, the levator arcus palatini assisted expansion of the buccal cavity by pulling the ventral part of the hyomandibular forwards (Gardiner 1967b). Normally this muscle is considered to have had its origin on the lateral wall of the braincase, as it does in *Polypterus* (Edgeworth 1935), and pressure of this muscle on the overlying dermal bones is held to be responsible for fragmentation of the suborbital in many palaeoniscoids. With the possible exception of *Redfieldius*, all redfieldiiform genera are characterized by a large unfragmented suborbital. As one would expect the levator arcus palatini to be well developed in any suction feeder, spread of the origin of this muscle onto the inner surface of the suborbital is likely, thus explaining the latter's size and undivided state. Supporting this reconstruction is the fact that in redfieldiids the suture between the suborbital and the anterior part of the preopercular is always orientated at right angles to the line of action of the levator arcus palatini. Such an alignment would ensure most efficient resistance to stresses created by contraction of the levator arcus palatini.

The most convincing evidence that the redfieldiids were suction feeders is the structure of the snout. As noted above, the ventral edge of the snout extends well beyond the tip of the mandible. The antorbital is large and extends posteriorly along the infraorbital bar. Both the antorbital and the rostral bear tubercles which, as suggested by Schaeffer (1967), would have helped support a fleshy lip. Such a lip would function to control the flow of water into the buccal cavity during abduction of the branchial basket.

In conclusion, various modifications of the redfieldiid skull are readily interpreted as adaptations towards suctorial feeding. Although the jaw gape was long, the mouth could function as a terminal suctorial organ when abduction of the branchial basket was achieved independently of abduction of the lower jaw.

Although small pieces of food were sucked into the buccal cavity, more conventional methods of feeding were also employed by the redfieldiids. The presence of teeth on the posterior border of the maxilla indicates that the lower jaw could be abducted to accommodate larger food masses. Adduction of the lower jaw is achieved by contraction of the adductor mandibulae. This muscle was completely enclosed by the dermal cheek elements, and the presence of an internal flange on the preopercular of *Ischnolepis* indicates that at least part of the adductor mandibulae had its origins on this bone in some redfieldiiforms.

One final redfieldiiform character remains to be considered, the presence of a single branchiostegal. The loss of the branchiostegal series in redfieldiiforms cannot be correlated with a forward shift of the jaw articulation for, as noted above, some genera have an oblique suspensorium. Loss of branchiostegals may possibly have allowed greater flexibility of the buccal floor, an important consideration in fish in which the buccal pump is more important than the opercular pump in maintaining a respiratory current. The single branchiostegal which is retained almost certainly acted to tie the ventral end of the opercular series to the throat region.

(c) Growth of the tail in *Brookvalia*, and some notes on palaeoniscoid body lobe squamation.

Wade (1935 : 27) has described the gradual appearance of scales in a growth series of *B. gracilis*. Here, a closer examination is made of the growth and development of the caudal region in that species. Four stages in the development of the tail in *B. gracilis* are represented by the following specimens: P.15810 (total length 31·5 mm); P.24710 (66 mm); U.S.G.D. 42 (76 mm); and an uncatalogued specimen in the University Museum of Zoology, Cambridge (115 mm); (Fig. 48).

In P.15810 the body, including the body lobe, is scaleless. The body lobe axis lies at 14° to the body axis, a lower angle than in larger specimens in which this angle is 26°. The dorsal border of the body lobe bears at least 11 paired basal fulcra which are short and broad (P.15810 and P.15807). There are 44 rays, 32 of which are contained in the ventral lobe. They are all unjointed and unbifurcated. Two

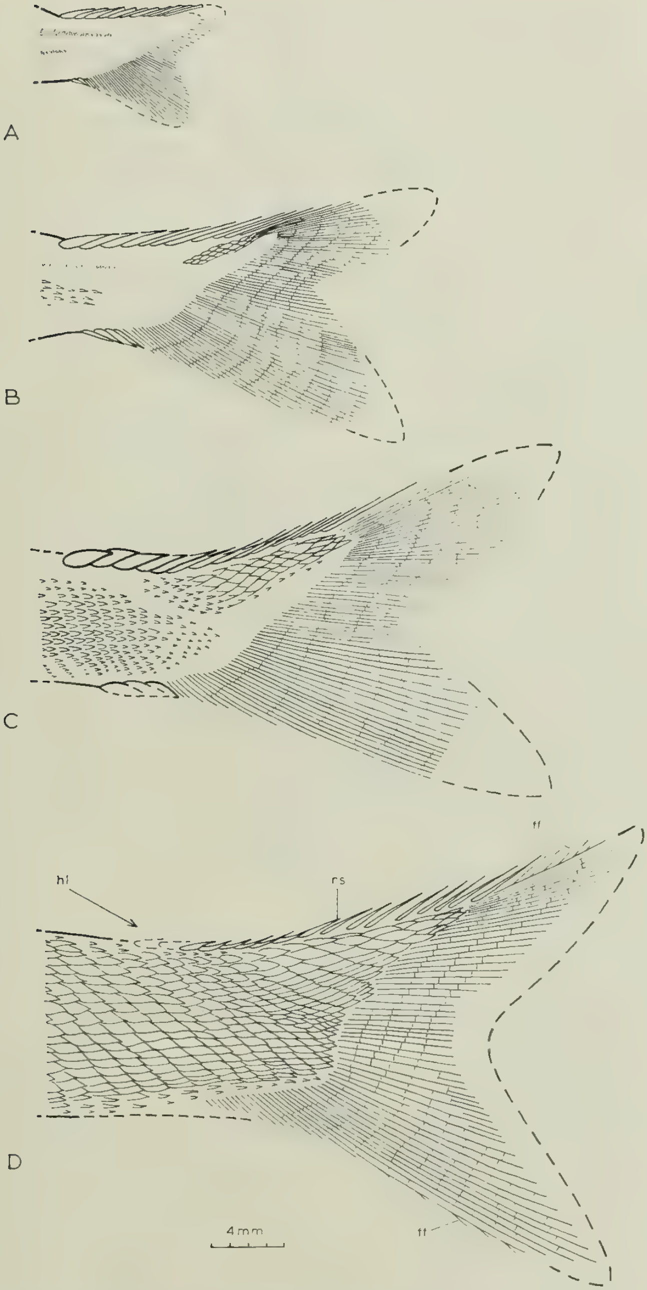
A
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FIG. 48. *Brookvalia gracilis* Wade. Series showing growth and development of caudal fin. (A) P.15810; (B) P.24710; (C) U.S.G.D. 42; (D) U.M.Z.C. uncatalogued.

bands of carbonaceous granules extend along the body flank and it is between these bands that body scales first appear (P.24710).

As the tail grows, several changes take place. The number of basal fulcra on the dorsal side of the body lobe increases from 11 to 15. This increase is certainly due to development of fulcra at the anterior end of the row, because anterior fulcra are smaller in large specimens of *B. gracilis* than in small ones. Also, in large specimens, posterior fulcra are inserted at the tip of the body lobe rather than further anteriorly, indicating that additional fulcra are developed at the posterior end of the row as well.

The number of fin rays increases from 44 (P.15810) to 63 (U.M.Z.C. uncatalogued). In spite of this, the number of rays present in the ventral lobe is fairly constant; 32 (P.15810), 38 (P.24710), 34 (U.S.G.D. 42) and 37 (U.M.Z.C. uncatalogued). The number of rays associated with the scales at the posterior tip of the body lobe is also fairly constant; 9 (P.24710), 10 (U.S.G.D. 42) and 11 (U.M.Z.C. uncatalogued) (in the smallest specimen, P.15810, the caudal lobe is scaleless). Thus the increase in the number of fin-rays is mainly due to addition along the ventral margin of the body lobe. In almost all specimens the long ventral rays have nine joints, and increase in length of the rays in larger individuals would seem to involve growth between joints, rather than the addition of new segments at the proximal end of the ray.

As noted above, very small specimens of *B. gracilis* are scaleless. When they first appear, scales are represented by narrow scale buds which gradually become broader until the characteristic leaf-shape of the fully grown scale is apparent. Scale buds first appear in the lateral line region and on the postero-dorsal part of the body lobe (P.24710). At a very early stage, the caudal lobe scales become closely associated with eight or nine dorsal caudal fin-rays. The body scales are directed posteriorly, while those on the body lobe point postero-dorsally. As the body scales extend posteriorly, they become postero-ventrally directed; in a similar way, the body lobe scales become postero-ventrally directed as they extend anteriorly (U.S.G.D. 42). As a result there is no marked hinge line where body and caudal scales meet; rather there is a band of postero-ventrally directed scales crossing the caudal peduncle (U.M.Z.C. uncatalogued).

Smith (1956) has suggested that the main function of the body lobe squamation in palaeoniscoids is protection. I doubt this conclusion. In some forms, e.g. *Birgeria* (Nielsen 1949), body scales are absent although those on the body lobe are retained. It seems likely that, if the organs of the body do not need the protection afforded by a scaly covering, scales would not be retained to protect the relatively unimportant blood vessels and nerves of the body lobe. It is far more likely that the main function of body lobe scales is to aid locomotion by providing an exoskeleton which holds the tail rigidly in the vertical plane. Strong supporting evidence of this view is the phenomenon present in palaeoniscoids known as 'reversal' of caudal scale rows. The body scale rows of all fish slope postero-ventrally. Kerr (1952) has shown that in *Lepisosteus* scales in the same scale row are more closely bound to one another by connective tissue than are scales of adjacent rows. Such an arrangement allows lateral flexibility of the body. In fish with heterocercal tails, efficient locomotion demands that the body lobe be laterally flexible whilst remaining rigid in the vertical plane, and this is achieved by close association of body lobe scales in rows which run antero-ventrally (Smith 1956). Antero-ventrally orientated, or reversed, body lobe scale rows are almost universally found in palaeoniscoids, and it is concluded that this is so for mechanical rather than for protective reasons.

Returning to *B. gracilis*, the mechanical function of the body lobe scales is stressed by the fact that, at an early stage in development, the posterior scales are closely associated with the dorsal caudal fin-rays. Rigidity of the caudal lobe is assisted by the basal fulcra which extend anteriorly along the dorsal side of the body lobe as far as the 'hinge' which crosses the caudal peduncle. The early development of basal fulcra and of caudal lobe squamation in *B. gracilis* suggests that these fish were active swimmers early in life.

Study of the development of the squamation in *B. gracilis* suggests very strongly that so called 'reversal' of caudal scale rows is, in this species at least, an apparent rather than a real phenomenon. As noted by Smith (1956 : 10), when scales meet 'heel to toe', scale rows can be regarded as running antero-ventrally or postero-ventrally. Such is the case in *B. gracilis*. The main reason for regarding postero-ventrally orientated scale rows as being homonomous (*sensu* Simpson 1961 : 93) with the body scale rows, is that the angle between body scale rows and the body axis (40°) is exactly the same as that between postero-ventral caudal scale rows and the axis of the caudal lobe. The difference in orientation of scale rows on body and body lobe is thus readily explained, not by reversal of scale rows, but by the fact that the 'tail does not at first during development turn upwards' (Moy-Thomas 1939 : 109), an occurrence noted above in the development of *B. gracilis*. Also it may be noted here that there is no reversal of direction of overlapping of scales on the caudal lobe of *B. gracilis*. Varied mechanical demands, for lateral flexibility at the caudal peduncle and for verticle rigidity of the caudal lobe, have therefore been met, not by reversal of caudal scale rows, but by variation in the orientation of individual scales within rows which bear constant angular relationships with the body and body lobe axes.

If the caudal squamation of *B. gracilis* can be readily interpreted without recourse to the concept of reversal of scale rows, it is likely that the squamation of other palaeoniscoids can be interpreted in a similar way. I believe this to be possible, even in the case of forms in which the hinge line marks a sudden change from body to body lobe scales. The tails figured here (Fig. 49) do not represent changes in squamation in closely related forms, but they do suggest how apparent reversal of body lobe scale rows may have taken place. *Paramesolepis tuberculata* (Fig. 49A) is clearly unspecialized in that postero-ventrally orientated scale rows ran from the body to the posterior tip of the body lobe. The scale rows become more horizontally orientated as they pass posteriorly, so that the long axes of the diamond-shaped posterior scales come to lie parallel with the caudal lobe axis. Such an arrangement gives the body lobe maximum rigidity in the vertical plane (Smith 1956). To achieve the same effect in *Turseodus dolorensis* (Fig. 49B), the ventral half of a single scale row (arrowed) is bifurcated. Similar bifurcation of body scale rows frequently occurs near the bases of the anal and dorsal fins in palaeoniscoids. In high aspect ratio tails, the need for such bifurcation is greater because the scale rows on the caudal peduncle must be turned through a larger angle if the posterior scale rows are to achieve the orientation which gives maximum rigidity to the caudal lobe. In *Pteronisculus stensioei* (Fig. 49C), one scale row has bifurcated twice (large arrow), and another only once. If such bifurcation takes place frequently, the postero-ventral orientation of the scale rows becomes obscured and the postero-dorsal rows of adjacent scales becomes more apparent. The illusion of scale row reversal is thus due to repeated bifurcation of postero-ventrally orientated scale rows. Finally, if repeated bifurcation only takes place posterior to a particular scale row, a distinct

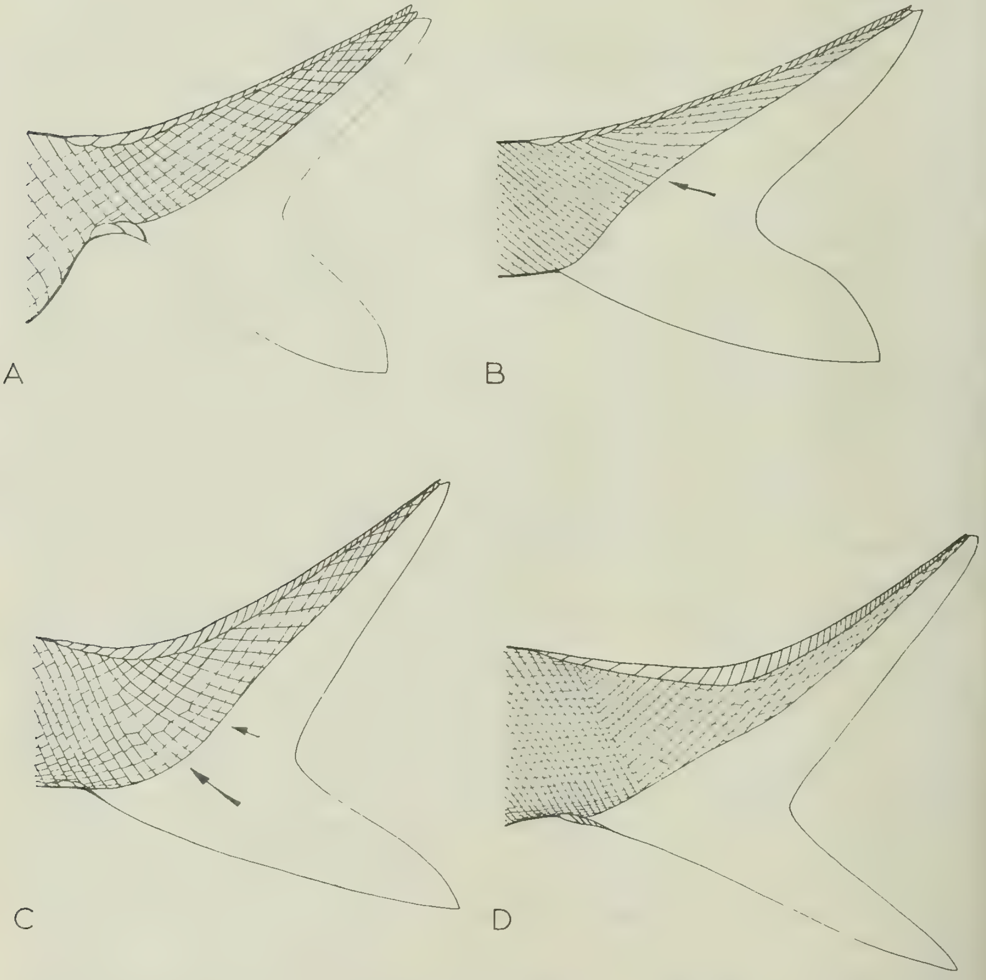

Fig. 49. The squamation of the body lobe in different palaeoniscoids. (A) *Paramesolepis tuberculata* (Moy-Thomas and Dyne 1938). (B) *Turseodus dolorensis* (Schaeffer 1967). (C) *Pteronisculus stensioei* (Nielsen 1942). (D) *Pygopterus nielseni* (Aldinger 1937).

boundary, or hinge line, between body and body lobe scales occurs at that scale row (e.g. *Pygopterus nielseni* Fig. 49D). Associated with the formation of a hinge line is the development of specially shaped transitional scales (see Smith 1956 : text-fig. 5).

The contrary view to that outlined above has recently been expressed by Patterson (1968 : 231), who argues: 'That this (reversal of caudal scale rows) is a real change in orientation of the scales is shown by the reversed direction of the overlapping of the scales and of the keels and peg-and-socket joints on the inner surface of the caudal scales'. The change in direction of overlapping in caudal scales noted by Patterson occurs in *Pholidophorus falcifer* (Schultze 1966 : text-fig. 11b). However, as the mechanical function of caudal scales has been relieved in pholidophorids by anterior development of the uroneurals (Patterson 1968), it is possible that their condition is recently evolved, and has little relevance to the condition seen in the Chondrostei.

(d) Classification of the Perleidiformes.

(i) *Colobodontidae.*

Of the genera included in this family (see Gardiner 1967 : 200), the following are sufficiently well known to provide a useful basis for discussion; *Colobodus, Dollopterus, Manlietta, Meidiichthys, Mendocinia, Meridensia, Perleidus, Pristisomus* and *Procheirichthys*. Several authors have indicated the various characters which these genera share (e.g. Brough 1931 and Schaeffer 1955) and it is generally accepted that they should be included in a single family. Whether or not the cleithrolepids should be included with these genera has been a more controversial topic and is discussed below. The most recent diagnosis of the family is that of Schaeffer (1955 : 19), to which nothing can be added here except that, in my opinion, it is doubtful that the antorbital is absent in colobodontids, as he suggests.

Although many characters are shared by various colobodontids, I cannot agree with Schaeffer (1955 : 15) that 'the known perleidids . . . have a relatively stable pattern'. For example, whereas *Colobodus koenigi* has twelve branchiostegal rays (Stolley 1920 : pl. 11, fig. 5), *Meidiichthys browni* has only three (Fig. 32). Again, *Manlietta crassa*, unlike other known genera, has no postrostral, the nasals meeting in the midline (Fig. 35). Whenever such variation occurs, it is usually possible to identify the more primitive condition by making comparisons with the condition typically found in palaeoniscoids. By employing such methods, a picture of the skull of a hypothetical colobodontid ancestor has been constructed (Fig. 50). This hypothetical fish will be called Y. Although Y has many characteristics typical of palaeoniscoids, it would nevertheless fall within the definition of the family Colobodontidae. Y will now be described briefly, so that the different ways in which known colobodontids have diverged from this type may be appreciated.

In Y the skull roof slopes gently towards the snout and is composed of three pairs of bones; narrow extrascapulars, square parietals and elongate frontals which are broad posteriorly and which are excavated along their ventral edges where they pass above the orbit. The dermopterotic is rectangular. In all colobodontid genera except *Meidiichthys* and *Meridensia* the skull roof is steeply inclined towards the snout, and in *Perleidus* the extrascapular is fairly broad. In *Meidiichthys* and *Perleidus* the dermopterotic is narrow.

In Y the opercular series is moderately inclined, and is composed of an opercular and a subopercular which are roughly equal in size. There are at least thirteen branchiostegal rays. In *Colobodus, Dollopterus, Manlietta* and *Mendocinia* the opercular and subopercular bones are also equal in size, but in *Meridensia* the opercular is slightly larger than the subopercular, and in all other genera the opercular is smaller than the subopercular. In *Colobodus* and *Meridensia* there are about eleven branchiostegals, but in all other genera there are six or fewer.

The cheek region in Y consists of a broad, high, 'r'-shaped preopercular, and a triangular dermohyal and suborbital. Variations of this pattern in colobontid genera include the loss of the dermohyal in *Meridensia* and probably also in *Procheirichthys*, subdivision of the preopercular in *Manlietta*, and fragmentation of the dorsal border of the preopercular in *Perleidus* to give two or three spiracular elements. In

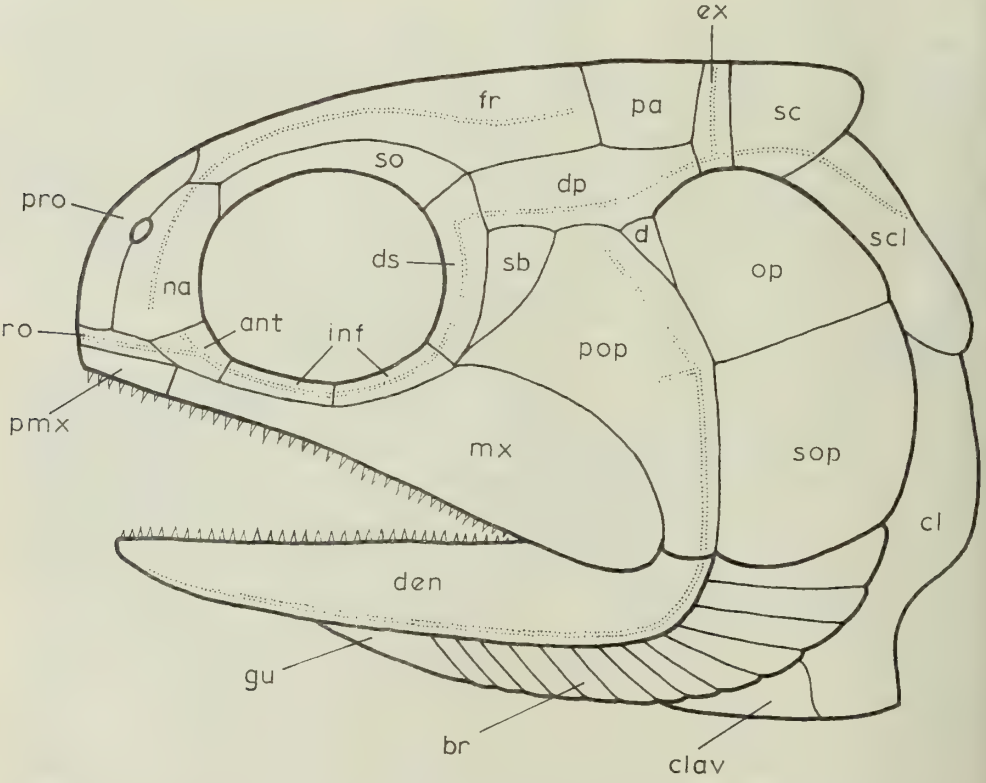

Fig. 50. Restoration of the skull and pectoral girdle of a hypothetical colobodontid ancestor.

all colobodontids the exact shapes of the preopercular and of the posterior part of the maxilla vary with the angle of the opercular series (cf. for example *Manlietta* with *Mendocinia*).

In Y the snout is composed of paired nasals which border the anterior orbital edge, and which are separated by a postrostral. The ventral part of the snout probably consists of paired rostrals, antorbitals and premaxillae, but this restoration is quite hypothetical because the ventral part of the snout in known colobodontids is rarely preserved. In *Meidiichthys* the postrostral is large and flat and gives the snout a profile with a blunt appearance which is unique amongst the colobodontids. In *Manlietta* the postrostral is lost and the nasals meet in the midline. As a result the nostrils have migrated to the ventral edge of the nasals and so parallel the condition seen in haplolepids (Westoll 1944).

The circumorbital bones are fairly stable in colobodontids. Y is figured with a single supraorbital element bordering the dorsal edge of the orbit. This is probably the condition seen in *Colobodus* and *Dollopterus*, while in other genera this bone has fragmented, usually into three elements. In *Meridensia* the supraorbitals are reduced so that the frontal borders the orbit for a short distance.

The pectoral girdle in Y consists of four paired dermal elements, 'D'-shaped suprascapulars, supracleithra, cleithra and clavicles. This same condition is seen only in *Meidiichthys*; in all other colobodontids the clavicles are either lost or fused to the cleithra. *Perleidus* and *Procheirichthys* are unusual in that their suprascapulars are widely separated, a condition which was probably present in the colobodontid ancestor of the Cleithrolepididae.

From the above comparisons it is clear that it is almost impossible to postulate phyletic lines within the family which include more than one known genus. The only exception to this may be the case of *Manlietta* and *Mendocinia* which are extremely similar in many respects. All genera have characteristics which may be thought of as being primitive in terms of the family as a whole, but no genus is consistently more primitive than any other genus. It may be concluded, therefore, that there may have been as many separate phyletic lines within the Colobodontidae as there are known genera. If this is so, the known genera represent but a small sample of a radiation which must have taken place in Triassic times.

(ii) *Cleithrolepididae and Hydropessidae*

The family Cleithrolepididae was erected by Wade (1935 : 47) to include three genera, *Cleithrolepis*, *Dipteronotus* and *Hydropessum*. To these can be added a fourth, *Cleithrolepidina*, erected in 1940 by Berg.

The phylogenetic relationship between the Cleithrolepididae and other chondrostean families is uncertain. Early views on this topic have been summarized by Brough (1931 : 269) and Wade (1935 : 47). In 1931 Brough, in a discussion of the systematic position of *Cleithrolepis minor* (now *Cleithrolepidina minor*, see above), says: 'The acceptance of the view that *Cleithrolepis* is a Platysomid derivative would involve the institution of a new family and, considering the doubt, it is better at present to regard it as a deep-bodied Perleidid' (1931 : 270). Four years later Wade did erect a new family saying ' . . . it is in the highest degree probable that

Cleithrolepis is derived, not directly from the Palaeoniscoids, but from the Platysomids, and that it should, therefore, be placed in a new family, the Cleithrolepidae . . .' (1935 : 48). In 1941 Wade modified this opinion somewhat. After a discussion in which he compared the species *Cleithrolepis minor* and *Cleithrolepis granulata*, he concluded that the two forms were different and that *C. minor* was a typical perleidid whereas *C. granulata* was quite distinct from the Perleididae (Colobodontidae). He continued '. . . we must conclude that if *C. minor* is a member of the Cleithrolepidae, this family must have arisen from some ancestor common to both Perleididae and Cleithrolepidae' (Wade 1941 : 392). Similar doubts about inclusion of *C. granulata* and *C. minor* in the same genus were expressed by Berg (1940), who separated them into distinct taxa, *Cleithrolepis* and *Cleithrolepidina*. However, he included both these genera in the family Cleithrolepidae [sic].

Most recent reviewers of actinopterygian classification have assumed that the Cleithrolepididae is a valid taxon and have favoured close association between it and colobodontids; Berg, Cleithrolepidae in Perleidiformes (1940 : 405); Lehman, *Cleithrolepis*, *Dipteronotus* and *Hydropessum* in Perleididae (1966 : 115–116); Gardiner, Cleithrolepididae in Perleidiformes (1967c : 190).

Five questions arise from this brief review of recent literature on cleithrolepids:

(1) Do *C. granulata* and *C. minor* represent separate genera?

(2) If so, can *Cleithrolepis* and *Cleithrolepidina* be included in one family, the Cleithrolepididae?

(3) If so, can other genera hitherto regarded as being similar to *Cleithrolepis* be included in the Cleithrolepididae, and if not, to what family do they belong?

(4) What are the evolutionary relationships of Cleithrolepididae?

(5) What are the evolutionary relationships of genera hitherto regarded as similar to *Cleithrolepis* but not included in the Cleithrolepididae?

These questions are discussed in turn here and at the beginning of the next section.

(1) Descriptions given above of *C. granulata*, *C. minor* and *C. extoni* show that two genera are present. *C. granulata* is included in the genus *Cleithrolepis* and *C. minor* and *C. extoni* in the genus *Cleithrolepidina*. The differences between these genera are not, however, those suggested by Berg (1940 : 405).

(2) Granted that *Cleithrolepis* and *Cleithrolepidina* are valid genera, can they be included in one family? Wade implied that this was not possible (Wade 1941b : 391–2) but his arguments have been discussed above with the conclusion that the differences noted by Wade merited at most generic status, and do not therefore merit separation of *Cleithrolepis* and *Cleithrolepidina* into separate families. Far more significant than the few differences between *Cleithrolepis* and *Cleithrolepidina*, are the large number of similarities between the two genera. The more important of these are:

1. The nasal is probably separated from the orbital edge.
2. The opercular is smaller than the subopercular.
3. A small triangular dermohyal present.
4. A slender lower jaw.
5. An accessory dermopterotic which lies ventral to the extrascapular.
6. The lack of a suprascapular.

7. The body shape—the dorsal side is strongly convex and forms a hump.
8. The unpaired fins have their origins close to the caudal fin and well posterior to the deepest part of the body.
9. The scales covering the pectoral region are orientated antero-ventrally.

This suite of characters strongly suggests that *Cleithrolepis* and *Cleithrolepidina* can be united within a single family.

(3) Before a diagnosis for the family Cleithrolepididae was constructed, other genera hitherto regarded as being similar to *Cleithrolepis* were examined to discover whether they share the suite of characters listed above. There are two such genera, *Dipteronotus* and *Hydropessum.*

Dipteronotus is poorly preserved. Its only characters which can be distinguished and which are found in the list above are: the body shape, the dorsal side is strongly convex, forming a hump, and the ventral side is also fairly strongly convex; and the positions of the unpaired fins, the dorsal and anal fins lie close to the caudal fin, well posterior to the deepest part of the body. No features can be discerned which suggest that *Dipteronotus* is not related to *Cleithrolepis* and *Cleithrolepidina. Dipteronotus* therefore may be provisionally viewed as being related to the cleithrolepids, but there is little strong evidence in support of this view.

Hydropessum is fairly well preserved and a new description has been given above. When the known features of this genus are compared with those of the cleithrolepids, many differences are at once apparent.

Cleithrolepis and *Cleithrolepidina*	*Hydropessum*
Nasal probably separated from orbital border.	Nasal bordering orbital border.
Opercular smaller than subopercular.	Opercular larger than subopercular.
A dermohyal present.	No dermohyal.
Lower jaw slender.	Lower jaw robust.
Accessory dermopterotic ventral to extrascapular.	No accessory dermopterotic.
Suprascapular absent.	Suprascapular present.
Dorsal side of body strongly convex and humped, ventral side convex.	Body diamond-shaped with roughly straight antero-dorsal, postero-dorsal, antero-ventral and postero-ventral sides.
Unpaired fins close to caudal fin, lying well posterior to deepest part of body.	Unpaired fins distant from caudal fin, lying with their anterior edges at the deepest part of the body.
Scales covering pectoral region orientated antero-ventrally.	Scales covering pectoral region orientated postero-ventrally.

It is therefore clear that, although *Hydropessum* is superficially similar to the cleithrolepids, there are enough differences between the two forms to warrant separation at familial level. The diagnosis of the Cleithrolepididae has been emended to include only the genera *Cleithrolepis*, *Cleithrolepidina* and *Dipteronotus*, and a new family, Hydropessidae, erected to include the genus *Hydropessum.*

(e) Evolution of the Perleidiformes.

The evolution of the Colobodontidae has been discussed above (p. 333). The relationships of the Cleithrolepididae and the Hydropessidae with the Colobodontidae will now be discussed in turn.

(i) *Cleithrolepididae.*

Early discussions on the origin of the cleithrolepids have emphasized the similarities of body shape between *Cleithrolepis* and *Platysomus* (Egerton 1864 : 3 and Woodward 1890 : 38). More recently, advocates of cleithrolepid–platysomid relationship have been Brough (1931 : 270) and Wade (1935 : 48). Some of the points of similarity between the two groups, such as the postero-dorsal slope of the skull roof and the presence of a hump anterior to the dorsal fin (Wade 1935) could be expected in any deep-bodied form whatever its ancestry, and therefore have little or no importance in this context. Another supposed point of similarity, the peculiar position of the post-temporal (suprascapular) (Brough 1931 : 270) can be discounted because the suprascapular is in fact lost in cleithrolepids. The bone identified by Brough as post-temporal in *C. minor* is here identified as an accessory dermopterotic. Lastly, because *Cleithrolepis granulata* has radials in advance of the anterior edge of the dorsal fin, Wade has suggested that its ancestor had a long dorsal fin, and that *Hydropessum* was this ancestor, linking *Cleithrolepis* with *Platysomus* (Wade 1935 : 48). This theory can now be shown to be untenable because the new description here of *Hydropessum* demonstrates that this genus differs from *Cleithrolepis* and must have had an entirely separate ancestry.

Although the case for platysomid and cleithrolepid relationship is weakened by evidence included here, there is, in my opinion, positive evidence which shows that cleithrolepids could not have evolved from platysomids. In *Cleithrolepidina* the maxilla is shallow, the infraorbital series narrow and the anterior border of the orbit close to the snout tip—all palaeoniscoid characters. The earliest representatives of the two platysomid families are Lower Carboniferous (Tournaisian) in age (e.g. *Paramesolepis* and *Platysomus*—Platysomidae, and *Cheirodopsis*—Amphicentridae) (Gardiner 1967a). In all these forms the maxilla is deep and triangular, the infraorbital deep and the snout tip elongated into a beak which extends a considerable distance antero-ventrally from the anterior orbital border (Moy-Thomas & Dyne 1938). Thus platysomids, as soon as they appear in the fossil record, have specialized features which preclude them from direct ancestry to the cleithrolepids.

Having ruled out the platysomids as possible cleithrolepid ancestors, it remains to discuss a more likely candidate. Brough (1931 : 269) admits that cleithrolepids have many features in common with colobodontids, but doubted that these were of phylogenetic significance because he was unable to point to any form with a body shape intermediate between the fusiform type seen in typical colobodontids and the deep type seen in cleithrolepids. However, there do not seem to be valid reasons for this doubt. The earliest cleithrolepids occur in rocks of Lower Triassic age. It is likely, therefore, that their ancestors were alive in Upper Permian times. But there are no known Upper Permian colobodontids, because their record, too, does not begin until Lower Triassic times. It is therefore impossible with the present state of knowledge to point to an actual cleithrolepid ancestor among the colobodontids. However, this does not disprove relationship between the two groups, and it remains possible that the two are descended from a common Permian ancestor. This possibility will now be examined.

Cleithrolepids and colobodontids such as *Meidiichthys* share a large number of features. The most primitive known cleithrolepid is *Cleithrolepidina*, and a list of features common to *Cleithrolepidina extoni* and *Meidiichthys browni* is impressive and certainly suggests common ancestry. They are:

1. A skull roof containing square parietals, a long narrow dermopterotic and a long frontal which is excavated above the orbit.
2. An upright opercular series containing an opercular which is smaller than the subopercular.
3. A single triangular dermohyal.
4. A single suborbital.
5. A preopercular bearing a horizontal sensory canal and with an antero-ventral process which extends between the maxilla and the infraorbital series.
6. The dermosphenotic, supraorbital and infraorbital elements are shaped similarly in the two forms.
7. A large, similarly shaped antorbital, anteriorly placed.
8. A snout composed of rectangular nasals, separated by a long postrostral, and paired antorbitals.
9. An essentially palaeoniscoid maxilla.
10. Unpaired fins with jointed, bifurcating rays which bear fringing fulcra.

There are, of course, differences between the two forms. Characters developed in *Cleithrolepidina extoni* but not in *Meidiichthys browni* can, in the main, be related to the evolution of a laterally compressed body and of a deep skull. These are:

1. A postero-dorsally sloping skull roof.
2. The absence of the suprascapular.
3. The development of an accessory dermopterotic.
4. The insertion of a postcleithrum in the pectoral girdle.

These characters are specifically related to the evolution of a greatly increased depth of the posterior part of the skull. In palaeoniscoids the dorsal part of the pectoral girdle must have been braced against the posterior part of the braincase through the suprascapular. This arrangement presumably remained unchanged throughout most of palaeonisciform history, for the 'D'-shaped suprascapular is one of the most conservative elements of the order. With the evolution of deep-skulled forms such as *Platysomus*, the suprascapular became enlarged so that the pectoral girdle could retain contact at its dorsal end with the braincase. A similar need in cleithrolepids appears to have been satisfied in a novel way. The suprascapular, instead of being enlarged, is lost entirely. This loss has been accompanied by the development of a new association, that between the dorsal end of the supracleithrum and an element here called an accessory dermopterotic. The accessory dermopterotic lies ventral to the extrascapular, unlike the suprascapular which lay posterior to it. Thus in cleithrolepids the pectoral girdle remains braced against the posterior

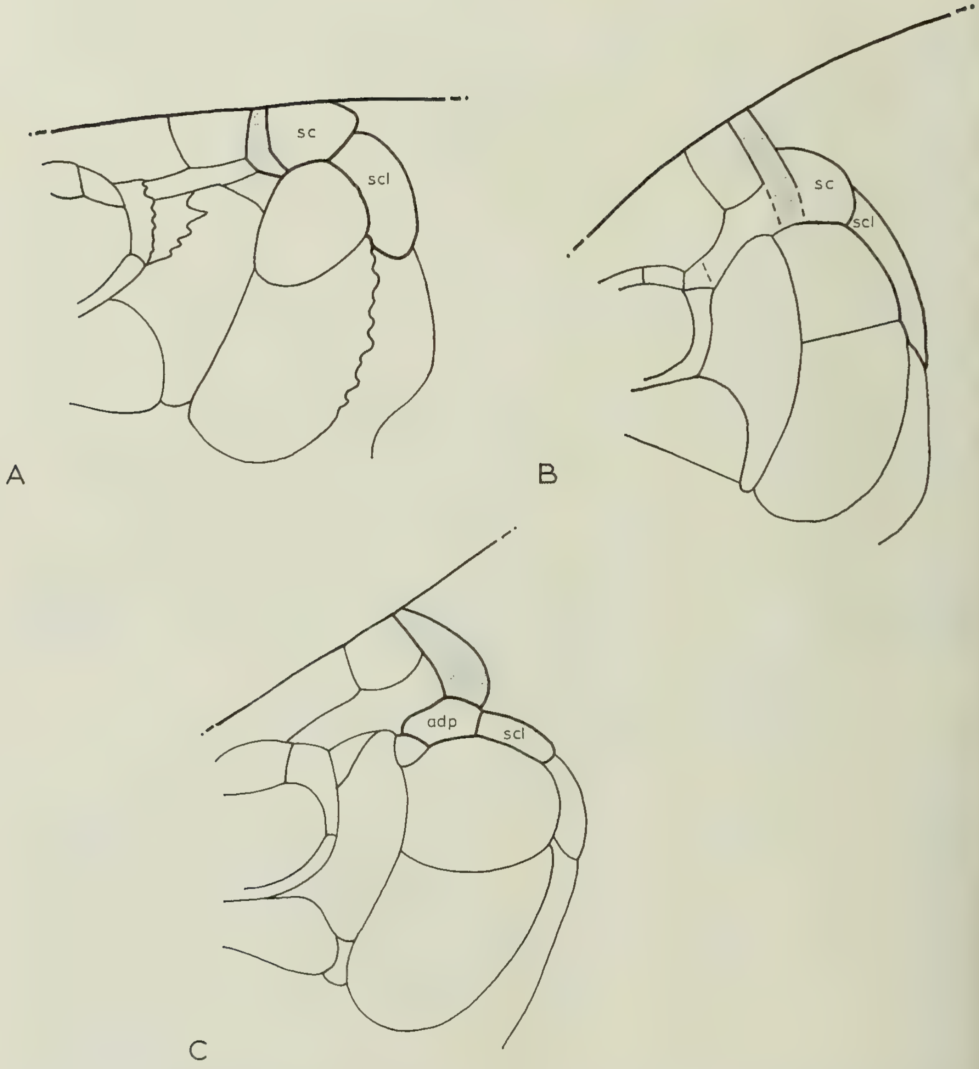

Fig. 51. Series showing the possible change in function of the extrascapular (stippled), during the evolution of a cleithrolepid from a colobodontid ancestor. The skulls are drawn to standard length, and orientated to the same base line to demonstrate the accompanying change of inclination of the skull roof. (A) *Meidiichthys browni* (Broom). (B) *Procheiricthys ferox* Wade. (C) *Cleithrolepidina extoni* (Woodward).

part of the skull, but in such a way as to allow dorsal extension of the dermal skull roof to evolve, in order to accommodate an increase in the depth of the body, without disturbing the pectoral girdle.

It is tempting to suppose that the accessory dermopterotic in cleithrolepids is homologous with the postspiracular seen in *Perleidus piveteaui* (Lehman 1952 : text-fig. 86) but the presence of part of the infraorbital sensory canal on the former bone in *Cleithrolepis granulata* makes this unlikely, and is the reason for identifying it as a fragment of the dermopterotic.

The change from the palaeoniscoid pectoral girdle to that of cleithrolepids involved not only rearrangement and loss of elements, but also a change in direction of the thrust acting through the supracleithrum. In palaeoniscoids the head of the supracleithrum butts against the roughly horizontal ventral edge of the suprascapular—the condition also seen in most colobodontids. In cleithrolepids the supracleithrum butts against the posterior edge of the accessory dermopterotic which faces posteriorly. Unfortunately there is no intermediate form known which shows how this change of structural organization took place. The nature of such an intermediate form is, however, suggested by the condition seen in *Procheirichthys* (Fig. 34) and *Perleidus* (Lehman 1952 : text-fig. 86) which have fairly deep skulls, though not as markedly deep as in cleithrolepids. In these genera the suprascapular elements are widely separated and probably occupied an area which bordered equally the ventral part of the extrascapular posterior margin and the postero-dorsal part of the opercular. Such an arrangement would cause the suture between the supracleithrum and the suprascapular to become more ventrally directed. It would probably also bring the dorsal end of the supracleithrum close to the posterior part of the dermopterotic. Once a firm connection was established between these two elements, the suprascapular would be deprived of its function and would be lost (Fig. 51).

The presence of a postcleithrum in *Cleithrolepidina extoni* is probably also related to the evolution of greater depth of the posterior part of the skull; its presence enables the pectoral girdle to span an increased distance effectively without excessive elongation of the cleithrum. Finally, in *Cleithrolepis granulata*, which has an even deeper skull than is seen in *Cleithrolepidina*, the extrascapular has fragmented into four separate elements.

There are a few other features seen in cleithrolepids but not in colobodontids, but they do not appear to discount relationship between the two groups. These are: a slender, toothless or almost toothless, lower jaw; a quadratojugal at the jaw articulation.

The first is of minor significance. Obviously, loss of teeth implies adoption of specialized feeding habits, but the type of lower jaw seen in cleithrolepids could readily be derived from that seen in colobontids (or almost any palaeoniscoid).

The development of a quadratojugal in cleithrolepids is perhaps more surprising. There is little evidence that such a bone is present in all palaeoniscoids, although it has been reported in *Cheirolepis* (Westoll 1937a) and *Pteronisculus* (Nielsen 1942). It would appear therefore that the quadratojugal in cleithrolepids has evolved *de novo*. An exact parallel in this respect is seen in the Haplolepididae (Westoll 1944).

One final difference between cleithrolepids and colobodontids is the probable presence in the former of an element which excludes the nasal from the orbital border. This is not a very significant difference because the cleithrolepid condition can readily be derived from that seen in colobodontids. In most of the cleithrolepid specimens studied, sensory canals were filled with calcite and so were readily visible. In no specimen was any trace of a sensory canal seen in the region immediately anterior to the orbit. It therefore seems likely that if a bone was in fact present in this area, it would probably consist of a supraorbital bone which had expanded ventrally, rather than an antorbital which had expanded dorsally.

It has been noted above that if the cleithrolepids are related to colobodontids, then their common ancestor was likely to have lived during Upper Permian times. The presence of a large number of branchiostegal rays in *Cleithrolepis granulata* supports this conclusion because all known colobodontids have a reduced number of branchiostegals and, if the ancestor to cleithrolepids was a colobodontid, it would need to be a primitive form which still retained about 13 branchiostegal rays. It may be noted here that the skull pattern seen in cleithrolepids could readily be derived from the hypothetical colobodontid ancestor Y (Fig. 50).

In conclusion therefore, the Cleithrolepididae, as defined here, is a family which shares many characters with colobodontids, and there is good evidence that the two groups had a common ancestor which, though not known, probably lived during Upper Permian times.

(ii) *Hydropessidae.*

Differences between *Hydropessum* and the cleithrolepids have been listed in the discussion of the Cleithrolepididae and Hydropessidae. The main reasons for concluding that *Hydropessum* merits recognition at familial level are as follows. The posterior part of the skull of *Hydropessum* is deep, but the supracleithrum retains contact with an enlarged suprascapular and is not modified as it is in cleithrolepids. More important, the bones of the cheek and upper jaw are specialized in shape and unlike those of any cleithrolepid, colobodontid or palaeoniscoid. Thus, although the condition of the pectoral girdle in *Hydropessum* suggests that it could be a primtive cleithrolepid, it is excluded from such a position by displaying other characters which are more advanced than those found in cleithrolepids. *Hydropessum* therefore is a representative of a phylogenetic line in which a deep body evolved, which is quite independent from that leading to cleithrolepids, and it remains to investigate the probable origin of the family.

Four families of deep-bodied fish should first be investigated in order to determine whether they may be related to the Hydropessidae; they are the Amphicentridae, Platysomidae, Dorypteridae and Bobasatraniidae. The first two of these families cannot be regarded as ancestral to the Hydropessidae because of the specialized nature of their snouts. *Hydropessum* has narrow infraorbitals and its snout retains proportions normally associated with unspecialized palaeoniscoids. In a similar way, relationship between the Dorypteridae or Bobasatraniidae and the Hydropessidae seems most unlikely. Both these families have specializations, such as heavy maxillae with crushing dentitions, which are not seen in the Hydropessidae.

One is therefore forced to look for possible ancestors of *Hydropessum* among fish with fusiform bodies, and once again, the colobodontids appear to be the most satisfactory. A comparison between *Hydropessum* and *Meidiichthys* produces the following list of similarities:

A single suborbital.

Similarly shaped dermosphenotic, supraorbital and infraorbital elements.

A similarly shaped orbit.

A snout consisting of paired nasals separated by a postrostral and bordering the orbital border; paired antorbitals or rostro-antorbitals and paired premaxillae.

This list is not as impressive as a list of similarities between cleithrolepids and colobodontids, but it should be emphasized that *Hydropessum* displays characters so aberrant that comparison with any other known form is not likely to produce convincing evidence of phylogenetic relationship. The difficulty of assessing the taxonomic position of *Hydropessum* is increased by lack of knowledge of the jaw articulation. Only part of the lower jaw of *Hydropessum* is preserved, and it is not clear whether it articulates with the quadrate near the posterior part of the maxilla or near the postero-ventral corner of the accessory preopercular. If the former condition is present, the unusual shape of the preopercular is readily interpreted as a means by which the jaw articulation has been brought forward. If this were so, it would be tempting to assume that there is a coronoid process on the lower jaw, but once again there is no evidence on this point.

In conclusion, therefore, there is a little evidence which suggests that *Hydropessum* evolved from colobodontids but, if this did indeed happen, there is good evidence suggesting that the phyletic line leading from colobodontids to *Hydropessum* was quite independent of that leading from colobodontids to cleithrolepids.

(f) Origin of the Refieldiiformes and Perleidiformes.

Early members of these orders are very similar to one another, and it is not surprising that genera from both were, until 1931, included in a single family, the Catopteridae (see Schaeffer 1967 : 329 for earlier classifications of these forms). Recent authors are of the opinion that there are few differences between the Redfieldiiformes and Perleidiformes. According to Schaeffer (1955) and Gardiner (1967c) these are the presence in the Redfieldiiformes of a single branchiostegal ray and an excess of fin-rays over radials in the dorsal and anal fins. In addition, Lehman (1952) notes the presence in perleidiforms of triturating teeth. There are in fact other valid differences between the orders, some of which were mentioned by Brough (1931 : 288). The most important of these is the presence of an unusual snout in the Redfieldiiformes, and the probable evolution of this feature will now be discussed in order to assess whether its presence gives any indication of the relationships of the group.

The redfieldiiform snout differs from that of palaeoniscoids in two important respects: the anterior orbital edge is bordered by the antorbital, not by the nasal, and there is a single large nostril, not two. Moreover, in the snout of the Brookvaliidae the antorbital is separated from the upper jaw margin by a premaxilla, while in the Redfieldiidae there is no premaxilla and the upper jaw margin is formed by the antorbital. The evolution of the brookvaliid and redfieldiid snouts from the

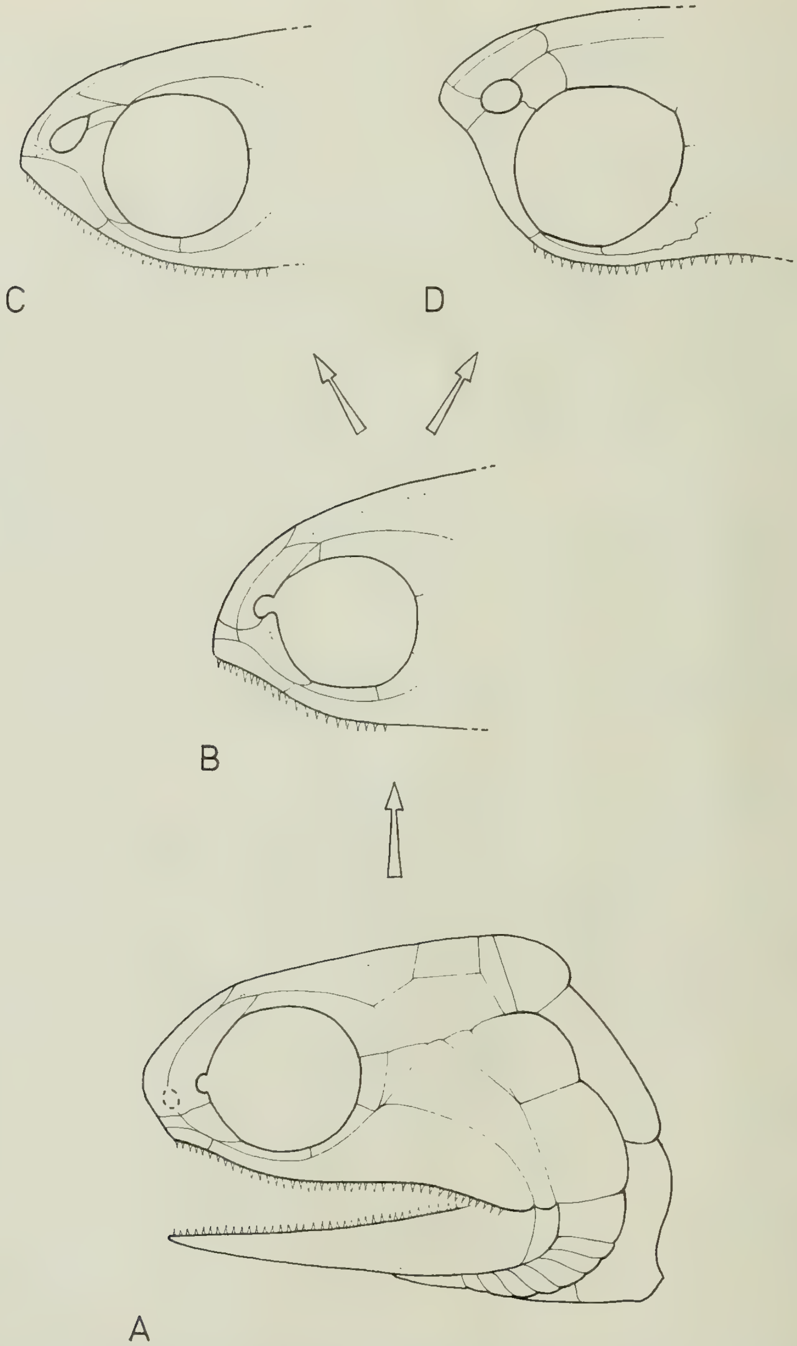

FIG. 52. The probable evolution of the redfieldiiform snout. (A) Hypothetical redfieldiiform ancestor. (B) Intermediate form in which dorsal extension of the dermosphenotic (or adnasal) begins to exclude the nasal from the anterior orbital border. (C) Brookvaliid type snout. (D) Redfieldiid type snout.

palaeoniscoid type is reconstructed in Fig. 52. The hypothetical snout (Fig. 52A) is typical of almost all palaeonisciform families, the anterior orbital edge being bordered by long nasals which are separated in the midline by a postrostral. Complete fragmentation of the rostro-premaxillo-antorbital is assumed to have taken place, for I have not seen any evidence which supports Gardiner's claim that 'the rostro-premaxillo-antorbital is still a single bone in the primitive members' (of the Redfieldiiformes) (1967 : 193). In the intermediate form (Fig. 52B) three changes may be noted:

(1) The anterior end of the dermosphenotic has begun to extend ventrally, excluding the dorsal part of the nasal from the orbital edge. (Fragmentation of the anterior end of the dermosphenotic, to give the redfieldiiform adnasal, may have been a synchronous event).

(2) The antorbital has begun to extend dorsally, thus excluding the ventral part of the nasal from the orbital edge, and is also beginning to take part in the posterior margin of the nostril. Such dorsal development of the antorbital has occurred several times during actinopterygian evolution, eg. in *Lawnia taylorensis* (Wilson 1953 : text-fig. 6), *Watsonulus eugnathoides* (Lehman 1952 : text-fig. 106), *Paracentrophorus madagascariensis* (Gardiner 1960 : text-fig. 66) and *Ichthyokentema purbeckensis* (Griffith & Patterson 1963 : text-fig. 6).

(3) The anterior nostril has either been lost or it has migrated around the ventral border of the nasal, and become confluent with the posterior nostril. Again, the latter event has been demonstrated in other actinopterygians (Gardiner 1963 : 315–318). Its occurrence in redfieldiids could possibly account for the large size of the nostril. Migration of the anterior nostril is usually correlated with loss of the postrostral, but this cannot be true in the case of the Redfieldiiformes, because the postrostral is almost invariably retained.

The intermediate form just described would readily give rise to the brookvaliid type of snout (Fig. 52C) if dorsal expansion of the antorbital continued until it met the adnasal, and to the redfieldiid type (Fig. 52D) if the same events were accompanied by the loss of the premaxilla. In both cases the nasal is reduced in size and becomes orientated so that it lies almost horizontally. As a result the nostril, which in most palaeoniscoids is ventral in position, assumes an unusually high position on the snout.

In a functional analysis of the redfieldiiform snout I have suggested that in both the brookvaliids and the redfieldiids many features can be related to bottom feeding. The changes which I now suggest must have taken place at an early stage, to produce the kind of snout seen in the Redfieldiiformes, may be related to this same habit. If the snout is frequently in contact with muddy river or lake bottoms, there would be an advantage in having the external nostril in a high position on the snout. This position has been achieved by shortening the nasal and by a change in its orientation so that its long axis lies roughly continuous with that of the frontal. Such alteration in the size and orientation of the nasal would lead to distortion of the orbit, and so would have necessitated the formation of a new anterior orbital edge; this has been achieved by dorsal growth of the antorbital.

Returning to the broader aspects of redfieldiiform relationships, it is likely that, although the redfieldiiform snout is unusual, it can be simply derived from a common palaeoniscoid pattern, and its presence does not debar close relationship of the order with the Perleidiformes. The hypothetical ancestor of the Redfieldiiformes (Fig. 52A) is very similar to that constructed for the Perleidiformes (Fig. 50); the only differences between the two are that in the latter the preopercular is broad, and the dermosphenotic borders the dorsal, rather than the posterior orbital edge. It may be concluded that it is quite likely that the two orders have origins in closely related palaeoniscoid groups.

Brough (1936 : 403) has suggested that the redfieldiiforms, at least, may be derived from a palaeoniscoid found in the Bekker's Kraal fauna, *Dicellopyge*. However, the holotype of *D. macrodentata*, the type species of the genus (Fig. 53), shows that this is unlikely for two reasons. Firstly, the area postero-dorsal to the orbit is covered, not by a single element (cf. Brough 1936 : text-fig. 1), but by a narrow dermosphenotic which is separated from the orbital edge by an equally narrow infraorbito-supraorbital element; secondly, an accessory opercular is present.

Gardiner (1967c) has suggested that a Carboniferous family, the Gonatodidae, is a probable ancestral group to the Redfieldiiformes and Perleidiformes. However, *Gonatodus* itself is an unlikely ancestral form for the Redfieldiiformes at least,

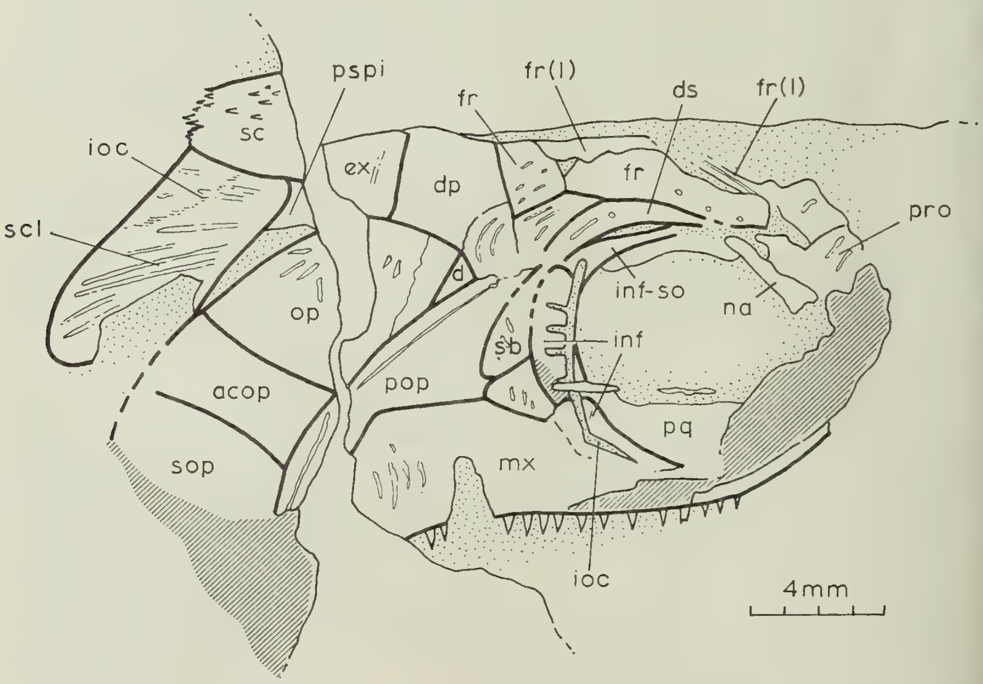

FIG. 53. *Dicellopyge macrodentata* Brough. G.N. 322: right side unless otherwise indicated.

because the posterior part of the maxilla is already shorter than in forms such as *Ischnolepis* and *Brookvalia*. I believe that the ancestry of both the Redfieldiiformes and the Perleidiformes will eventually be found among the Elonichthyidae, Acrolepididae, Rhadinichthyidae complex of families.

IV. SUMMARY

1. The Redfieldiiformes and Perleidiformes from Triassic localities at Bekker's Kraal (Scythian of South Africa) and Brookvale (probable Ladinian of New South Wales) are redescribed. In addition, *Ischnolepis*, a redfieldiiform from Zambia, is redescribed.
2. The order Redfieldiiformes is divided into three families; the Brookvaliidae, the Redfieldiidae and the Schizurichthyidae *nov.*
3. The Brookvaliidae contains the following well known genera: *Ischnolepis*, *Atopocephala*, *Brookvalia* and *Phlyctaenichthys*. They are characterized by large orbits, narrow crescent-shaped dermosphenotics, a snout in which the antorbital is excluded from the upper jaw margin by a toothed element, and by a slender lower jaw. *Dictyopleurichthys* and *Beaconia* are synonymized with *Brookvalia*, and *Brookvalia parvisquamata* is shown to be a junior synonym of *B. gracilis*.
4. The Redfieldiidae contains the following well known genera: *Daedalichthys*, *Helichthys*, *Geitonichthys*, *Molybdichthys*, *Redfieldius*, *Cionichthys*, *Synorichthys* and *Lasalichthys*. They are characterized by small orbits, deep rectangular dermosphenotics, a snout in which there is no premaxilla and in which the antorbital borders the upper jaw margin, and by a short, robust lower jaw.
5. A new family, the Schizurichthyidae, is erected to contain the genus *Schizurichthys* which, although superficially similar to the brookvaliids, is unique in having scales which articulate with one another with peg-and-socket joints, and a caudal fin which has a separate epaxial lobe.
6. The order Perleidiformes is divided into four families; the Aetheodontidae (which is not discussed here), the Colobodontidae, the Cleithrolepididae and the Hydropessidae *nov.*
7. The Colobodontidae contains the following well known genera: *Dollopterus*, *Colobodus*, *Mendocinia* and *Perleidus* which are not found at either Bekker's Kraal or Brookvale, and *Meidiichthys*, *Procheirichthys* and *Manlietta*. Each colobodontid genus represents a separate phyletic line of a radiation which had Permian origins.
8. The Cleithrolepididae contains two well known genera, *Cleithrolepidina* and *Cleithrolepis*. *Cleithrolepis* differs from *Cleithrolepidina* in having an extremely deep snout and maxilla, and a fragmented extrascapular. *Cleithrolepis extoni* is shown to be a member of *Cleithrolepidina*.
9. A new family, the Hydropessidae, is erected to contain the genus *Hydropessum* which differs from the cleithrolepids in the structure of its skull and pectoral girdle, in the position of its unpaired fins, and in the orientation of the scales in its pectoral region.

10. The interrelationships between the redfieldiiform and perleidiform families are summarized in Fig. 54.
11. A functional analysis is made of the redfieldiiform skull, and it is concluded that in the Redfieldiidae food was obtained by using the buccal cavity as a suction pump.
12. The growth and development of the tail in *Brookvalia gracilis* is described,

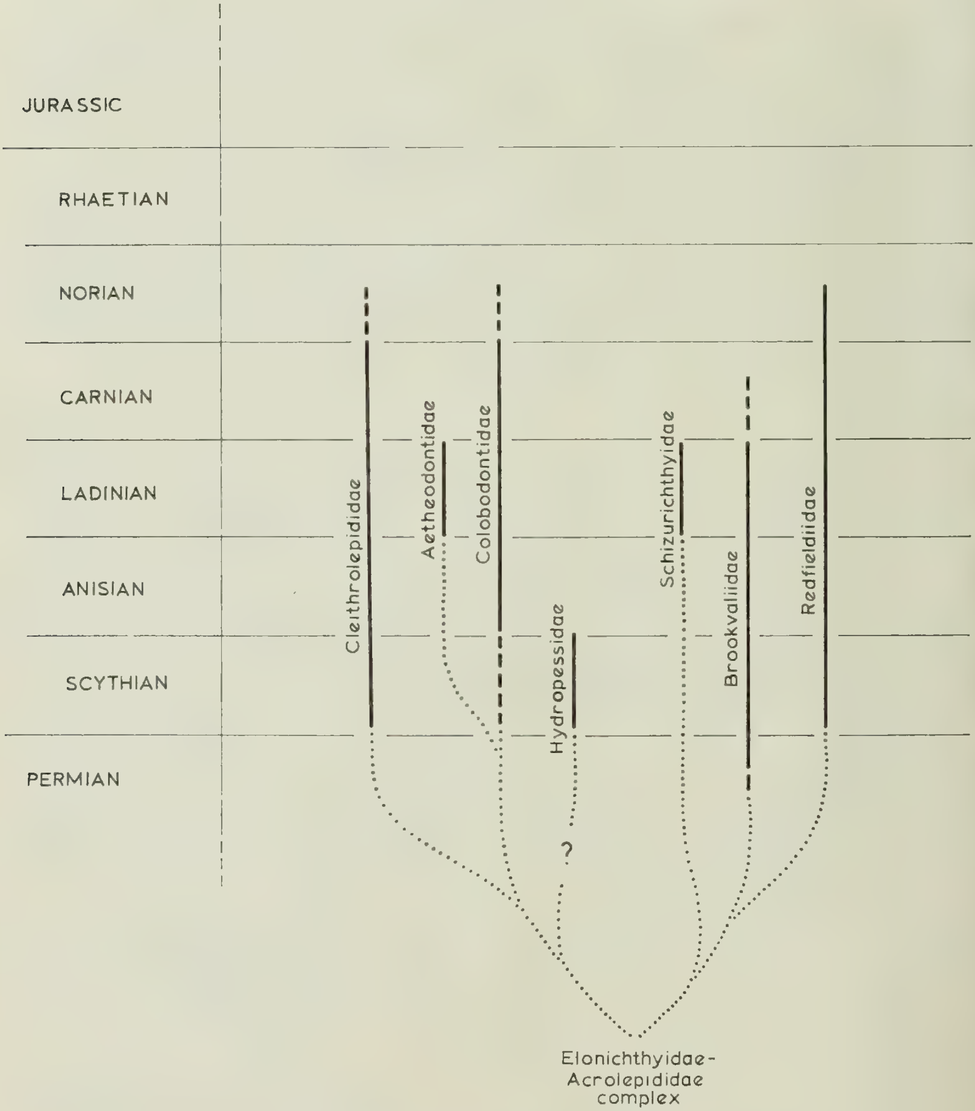

FIG. 54. Probable phylogenetic relationships between the redfieldiiform and perleidiform families.

and the caudal lobe squamation in palaeoniscoids is discussed. It is concluded that reversal of caudal lobe scale rows does not occur in palaeoniscoids, and that the formation of a hinge line across the base of the caudal peduncle is the result of bifurcation of scale rows in the ventral region of the caudal lobe.

V. ACKNOWLEDGEMENTS

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VI. ABBREVIATIONS

The following abbreviations either indicate the name of an institution, or are used by the institution indicated as a prefix to the catalogue numbers of specimens in their collections:

AM.MF	The Australian Museum, Sydney.
A.M.N.H.	The American Museum of Natural History, New York.
B.M.(N.H.)	British Museum (Natural History), London.
D.M.S.W.	D. M. S. Watson collection (housed at the University Museum of Zoology, Cambridge).
F.	The Australian Museum, Sydney, unless otherwise indicated. (Some specimens at the Sedgwick Museum, Cambridge bear F.—catalogue numbers.)
G.N.	University Museum of Zoology, Cambridge.
G.S.M.	Institute of Geological Sciences, London.
L.	Manchester Museum.
P.	British Museum (Natural History), London.
S.A.M.	South African Museum, Cape Town.
S.U.P.	University of Sydney, Geology Department.
U.M.Z.C.	University Museum of Zoology, Cambridge.
U.S.G.D.	University of Sydney, Geology Department, unless otherwise indicated. (Some specimens at the University Museum of Zoology, Cambridge, bear U.S.G.D.-catalogue numbers.)

ABBREVIATIONS USED IN THE FIGURES

a	antopercular	iop	interopercular
acop	accessory opercular	(l)	left side
ad	adnasal	ll	lateral line
adp	accessory dermopterotic	lpop	lamina of the preopercular
an	angular	meck	meckelian bone
ant	antorbital	mx	maxilla
apop	accessory preopercular	na	nasal
art	articular	no	nostril border or nostril
b	branchial arch element	op	opercular
bf	basal fulcra	pa	parietal
br	branchiostegal ray	par	parasphenoid
cl	cleithrum	pcl	postcleithrum
clav	clavicle	pmx	premaxilla
co	coronoid	po	postorbital
d	dermohyal	pop	preopercular
den	dentary	pq	palatoquadrate
dp	dermopterotic	pro	postrostral
dpal	dermopalatine	proc	process
dpt	dermometapterygoid	pspi	postspiracular
ds	dermosphenotic	qj	quadratojugal
ecomm	ethmoid commissure	(r)	right side
ecpt	ectopterygoid	ro	rostral
ept	endopterygoid	ro-ant	rostro-antorbital
ex	extrascapular	ro-pmx	rostro-premaxillary
fam	foramen for the adductor mandibulae	rs	ridge scale
		sb	suborbital
ff	fringing fulcra	sc	suprascapula
fr	frontal	scl	supracleithrum
gu	gular plate	so	supraorbital
hl	hinge line	soc	supraorbital sensory canal
hym	hyomandibular	t	teeth
inf	infraorbital	tm	tube containing mandibular canal
inf-so	infraorbito-supraorbital		
ioc	infraorbital sensory canal	vo	vomer

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LOWER PALAEOZOIC GREEN ALGAE FROM SOUTHERN SCOTLAND, AND THEIR EVOLUTIONARY SIGNIFICANCE

G. F. ELLIOTT

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GRAHAM FRANCIS ELLIOTT

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By G. F. ELLIOTT

CONTENTS

Page
I. INTRODUCTION 358
II. SYSTEMATIC DESCRIPTIONS 358
  Class Chlorophycaceae 358
    Order Siphonales 358
      Family Codiaceae 358
        Genus *Dimorphosiphon* Høeg. 358
          D. rectangulare Høeg 358
    Order Dasycladales 360
      Family Dasycladaceae 360
        Tribe Dasyporelleae Pia 360
        Genus *Vermiporella* Stolley 360
          V. eisenacki sp. nov. 361
          V. cf. *borealis* Høeg 361
          V. sp. 361
        Genus *Intermurella* gen. nov. 361
          I. scotica sp. nov. 361
        Genus *Dasyporella* Stolley 362
          D. cf. *norvegica* Høeg 362
        Genus *Novantiella* gen. nov. 362
          N. ordoviciana sp. nov. 362
        Tribe Cyclocrineae Pia 363
        Genus *Mastopora* Eichwald 363
          M. parva (Nicholson & Etheridge) Pia . . 364
          M. fava (Salter) Stolley 366
    Order Receptaculitales 367
  Family Receptaculitaceae 367
        Genus *Ischadites* Murchison 367
          I. sp. 367
III. THE EVOLUTION OF REPRODUCTIVE STRUCTURES OR ORGANS IN THE DASYCLADALES 368
  1. Introduction 368
  2. Patterns of Dasycladacean Reproductive Structure . 368
  3. The Reproductive Ontogeny of the Dasycladaceae . . 370
  4. The Component Factors of Dasycladacean Evolution . 370
  5. Conclusions 372
IV. REFERENCES 372

ABSTRACT

Ordovician and Silurian green algae (Chlorophyta) from the Girvan area, southern Scotland are described. Species are described recorded and discussed of the genera *Dimorphosiphon* (Codiaceae); *Vermiporella, Intermurella* gen. nov., *Dasyporella, Novantiella* gen. nov., *Mastopora* (Dasycladaceae); and *Ischadites* (Receptaculitaceae). The differences between *Dimorphosiphon* and the similar Recent genus *Halimeda* are discussed. The alleged reproductive structures of *Mastopora parva* are considered inorganic in origin. An early non-calcified growth-stage of *M. fava* is described. *Ischadites* is compared with the living non-calcified *Dictyosphaeria*.

The primitive character of this algal flora is related to the main course of Dasycladalean evolution. This is explained in terms of progressive elaboration in ontogeny and phylogeny of the vegetative thallus, against the unaltered reproductive mechanism of large-nucleus fragmentation to give peripheral reproductive bodies, the whole documented for the fossils by very variable calcification as between different genera. The progressive elaboration of Dasycladacean reproductive structures during evolution conferred no apparent advantage on them as compared with other algae.

INTRODUCTION

ALTHOUGH the Ordovician of the Girvan area of Southern Scotland is well-known for the ubiquitous blue-green alga *Girvanella* and the red alga *Solenopora*, little attention has been paid to the interesting green algae which occur there. Currie & Edwards (1943) described species of Girvan *Mastopora* (Dasycladaceae) in some detail, and it was a re-examination of this material in the Mrs Robert Gray collection, and also other specimens from a part of the Garwood Collection, both housed in the British Museum (Natural History), that led to the present study. This has proved unexpectedly rewarding, for although the programme of thin-sectioning did not yield the exact evidence sought for the initial enquiry, it has revealed much else, and has helped towards a fresh evaluation of the evolution of the Dasycladales.

Part II

SYSTEMATIC DESCRIPTIONS

Class *CHLOROPHYCACEAE*

Order SIPHONALES Blackman & Tansley, 1902

Family **CODIACEAE** Kützing orth. mut. Hauck, 1884

Genus ***DIMORPHOSIPHON*** Høeg 1927

Dimorphosiphon rectangulare Høeg

Pl. 1; Pl. 2, figs 4, 5.

Remarks. This very characteristic species, familiar from the Norwegian Ordovician, is now recognized from Scotland. It occurs in the type Craighead Limestone, Caradocian, Upper Ordovician, and in the collections studied is represented by random thin-sections of segments (Pl. 2, figs 4, 5). These show the very coarse medullary threads and the thinner lateral or cortical threads. Segment diameters vary from 2·21–2·6 mm, with an incomplete segment length of 6·24 mm seen. The diameters of the central threads are about 0·234 mm, and those of the lateral threads 0·052–0·065 mm. About 21 central threads are seen in one example. These examples compare well with the Norwegian type-material, where segments have a length of 10 mm, and diameter of 2·5 mm, central threads show a diameter of 0·2–0·3 mm, and lateral threads 0·08–0·12 mm, with from 7 to 25 central threads seen in different transverse sections.

Discussion. The striking resemblance between the Ordovician *Dimorphosiphon* and the later *Halimeda* (Cretaceous–Recent) was discussed by Høeg in his original description (Høeg, 1927) and has been noted by all subsequent workers (e.g. Johnson 1961). The long straight coarse medullary threads and divergent finer lateral threads of the Ordovician genus are surprisingly reminiscent of those of the more familiar and widely-distributed *Halimeda*.

However, there are important points of difference.

1. In *Dimorphosiphon* the cortical (lateral) branches are fewer, straighter and only occasionally achieve the characteristic repeatedly swollen terminal divisions of *Halimeda*, and these are never crowded as in *Halimeda*.
2. The internodes (connecting threads between calcified segments), are not known for *Dimorphosiphon*, but although some communication or division of main threads must have occurred (since different segments often have different numbers of threads), yet the several complex internode patterns described for living *Halimeda* (Hillis 1959) are very unlikely to have been present in *Dimorphosiphon*. This latter seems to have been generally more simple in structure.
3. So far as is known, *Dimorphosiphon* did not show the great variety of segment-shape (cf. Hillis 1959) of *Halimeda*.

Dimorphosiphon thus appears to represent an early achievement of one of several of the thread- and growth-patterns seen in segmented codiaceans, which I have listed elsewhere (Elliott 1970*a*, Key p. 331). When this particular pattern reappears later in *Halimeda*, possibly as a result of hybridization in the Cretaceous between the Mesozoic *Boueina* and *Arabicodium* stocks (Elliott 1965) it is much more elaborate, and from Upper Cretaceous onwards *Halimeda* has replaced the other calcified segmented codiaceans in a vigorous evolutionary diversification through Tertiary to Recent. It thus represents a later much more successful varied and elaborate achievement of the thread- and growth-pattern seen in *Dimorphosiphon*. Unlike the latter, which became extinct, *Halimeda* has replaced not merely other calcified codiaceans in the appropriate marine ecologies but in great part dasycladaceans as well, (Elliott 1968, 100–101).

Order DASYCLADALES Pascher 1931
Family **DASYCLADACEAE** Kützing orth. mut. Hauck, 1884
Tribe **DASYPORELLEAE** Pia, 1920
Genus ***Vermiporella*** Stolley 1893

DIAGNOSIS (after Stolley emend. Pia). Branching curved calcareous tubes with variable wall-thickness and proportionally large stem-cell cavity (d/D ratio 60% or more). Evidence of primary branches only, the pores usually widening outwards in diameter, and set at or near right-angles to the stem-cell. The pores are irregularly close-set, and not arranged in verticils. Palaeozoic, especially Lower Palaeozoic. Type-species *V. fragilis* Stolley.

Vermiporella eisenacki sp. nov.

Pl. 3, figs 1, 2.

DIAGNOSIS. *Vermiporella* species with an external tube-diameter of about 0·4–0·5 mm, probably anastomosing like *Vermiporella* sp. of Eisenack (1936). Ordovician of Scotland.

DESCRIPTION. Forked, bent, branching and probably anastomosing tangled hollow calcareous tubular thallus. External diameter 0·39–0·52 mm, narrowing slightly between points of branching or junctions where it widens. Calcification thin and rather variable, so that the relation of inner to outer diameter of the tubular structures is 60–70%. The branch-pores are set irregularly but closely in the calcification, not in verticils, with the pore-interstices wider than the outer pore-diameters. In section the pores are seen to widen from within outwards; they are rather variable in size but often show an outer diameter of 0·040 mm.

HOLOTYPE. The specimen figured in Pl. 3, fig. 2, from the Stinchar Limestone, Caradocian, Upper Ordovician: Tramitchell Quarry, Girvan, Scotland. British Museum (Natural History), Department of Palaeontology, reg. no. V.54162b.

PARATYPES. The specimen figured in Pl. 3, fig. 1, and one other; same locality and horizon as the holotype. Reg. nos. V.54162a, V.54162b.

REMARKS. *Vermiporella* is an extremely difficult genus for which to allocate species. Specimens allotted to it consist of primitive very simple dasycladacean tubes of protean morphology, perforated by very variable branch-pores, and normally occurring fossil in a fragmentary condition. Stolley's description of the type-species *V. fragilis* (Stolley, 1893) is inadequate by present-day standards, and the holotype is missing. For this reason most workers (e.g. Høeg, 1932; Gnilovskaya, 1965) have classified their material largely on differences in the local florules studied.

V. eisenacki is very similar to the *Vermiporella* sp. described by Eisenack (1936). This came from a silicified Silurian Baltic erratic, and was isolated three-dimensionally by acid treatment, the thallus being seen as tangles of bent, branched, anastomosing tubes, of about 0·45–0·60 mm diameter. *V. eisenacki* differs in showing clear pore-structure, a smaller tube diameter, and in being accurately localized in the

Ordovician. Both these species differ from *V. affluens*, *V. acerosa*, and *V. wesenbergensis* (all of Gnilovskaya, 1965), from *V. borealis*, *V. inconstans*, and *V.* sp. (all of Høeg, 1932), and from *V. canadensis* Horne & Johnson (1970).

Vermiporella cf. ***borealis*** Høeg

Pl. 5, fig. 1.

REMARKS. Høeg (1932) described this Norwegian species and records 'abundant, but rather poorly preserved fragments' of this species in the type Craighead Limestone, Caradocian, Upper Ordovician. In the Scottish thin-sections now studied, rather variable vermiporellid fragments are common. These are presumably the same as those on which Høeg based his identification, and one is now figured as *V.* cf. *borealis*.

Vermiporella sp.

Pl. 5, fig. 3.

REMARKS. A large very thin-walled *Vermiporella* sp. occurs uncommonly in the Stinchar Limestone (Caradocian, Upper Ordovician), of Benan Burn, Barr, Ayrshire. It is quite distinct from the common Stinchar Limestone *V. eisenacki*, but the material available is insufficient for description.

Genus ***INTERMURELLA*** gen. nov.

DIAGNOSIS. Large vermiporellid dasycladacean (external diameter of nearly 2 mm) differing from *Vermiporella* in being straight, slightly curved or slightly sinuous, and not branching, forking or anastomosing. Ordovician of Scotland.

TYPE-SPECIES. *I. scotica* sp. nov.

Intermurella scotica sp. nov.

Pl. 3, fig. 1; Pl. 4.

DIAGNOSIS. *Intermurella* of about 2 mm external diameter, d/D ratio 55–60%; the close-set non-verticillate pores are irregularly funnel-shaped, widening outwards.

DESCRIPTION. Irregularly-sinuous elongate-claviform hollow calcareous dasycladacean tube, circular in cross-section, length of 8·06 mm, (holotype) with external diameter of 1·90 mm, internal diameter of 1·04 mm, d/D 55–60%. Smaller examples occur; also a larger example of 10·92 mm length (incomplete). The pores are irregularly close-set, and not in verticils. In section the pores are variable irregular funnel-shaped, with narrow insertions to the stem-cell cavity and widening suddenly to cup-shaped at about halfway in the wall-thickness, so that inside the pore-interstices are wider than the pores and outside the pores wider than the interstices. Inner pore-diameters are 0·026–0·040 mm, maximum pore-diameters, at or just below the outer surface, are about 0·090 mm. About 40 pores are seen in an average transverse section.

Holotype. The specimen figured in Pl. 4, fig. 1, from the Craighead Limestone, Caradocian, Upper Ordovician: Craighead, nr. Girvan, Ayrshire, Scotland. Reg. no. V.55302a.

Paratypes. The specimens figured in pl. 4, figs 2, 3; same locality and horizon, reg. nos. V.55302b, c.

Remarks. *Intermurella*, though primitive in structure, is a distinctive new genus. The name refers to the type-area, in southern Scotland, this being situated in the country between the Roman Hadrianic and Antonine Walls.

Genus ***DASYPORELLA*** Stolley 1893

Dasyporella cf. ***norvegica*** Høeg

Pl. 2, figs 1, 2.

Description. Thick-walled bluntly-claviform, almost cylindrical, hollow calcareous tube with closed rounded termination, circular in cross-section. The largest example showed an external diameter of 1·56 mm, and internal diameter of 0·52 mm, giving a d/D ratio of 33%. In transverse cut about 70 near-straight closely-packed radial branches are seen: branch-diameter is about 0·020 mm. An example with length of 2·03 mm, showed external diameter of 0·91 mm, internal diameter 0·39 mm, with d/D ratio of 43%.

Remarks. This species is very similar to the Scandinavian *D. norvegica* Høeg, which differs only in larger size (external diameter 2·25–4·00 mm). The Scottish fossils may be merely small examples of the Norwegian species. They occur in the type Craighead Limestone, Caradocian, Upper Ordovician.

Høeg (1961) discussed Californian Silurian algae referred by Johnson & Konishi (1959) to *Dasyporella*, but showing a different, non-dasycladacean, branch-structure to *D. norvegica* which is less well-preserved. Stolley's type-specimen of the type-species *D. silurica* is missing. In spite of the uncertainties discussed in full by Høeg, it seems best to conclude with him that probably the Californian algae belong to a different genus to *D. norvegica*, and the Scottish specimens now described are compared with the species *D. norvegica* as conventionally understood.

Genus ***NOVANTIELLA*** gen. nov.

Diagnosis. Cylindrical calcareous dasycladacean tube with wide central cavity and non-verticillate close-pressed swollen primary side-branch cavities separated only by very thin calcification. Ordovician of Scotland. Type-species *Novantiella ordoviciana* sp. nov.

Novantiella ordoviciana sp. nov.

Pl. 6.

Diagnosis. *Novantiella* of 10 mm length or more, external diameter up to 2·26 mm, d/D ratio 53–63%; diameters of primary branch-cavities are 10 or 11 times or more the thickness of the thin separating calcification.

DESCRIPTION. This is a fragile very lightly-calcified dasycladacean tube. A crushed example measures 10·4 mm in length. Transverse sections of uncrushed examples show circular cross-section with external diameters ranging from 1·69–2·26 mm. The stem-cell cavity is moderately wide, the relation of internal to external diameter varying from 53–63%. The wall consists essentially of the cavities left by the side-branches with very little intervening calcification. These branch-cavities are very close-packed, irregularly set, cylindrical in form, rounded polygonal in cross-section, with a length (at right-angles to the stem-cell) varying from 0·31–0·44 mm in different sized examples, but approximately consistent in each separate example. Diameters in cross-section range from 0·091–0·117 mm wide; they are a little more variable, due to crowding, than the lengths.

The calcification which outlines these structures is very thin. It consists of straight, near-parallel calcareous walls of 0·010 mm or often less thickness between branches, terminating outwards at the curved plane of the cylindrical thallus without any elaboration whatsoever. At the inner, stem-cell cavity termination they are very slightly clubbed (to twice wall-thickness or less); this is interpreted as a very slight development of the usual initial constriction of side-branches coming off a dasycladacean stem-cell.

HOLOTYPE. The specimen figured in pl. 6, fig. 1, from the Lower Ardmillan Series, Balclatchie Group, Caradocian, Upper Ordovician; Balclatchie, Girvan, Ayrshire. Reg. no. V.16124a.

PARATYPE. The specimen figured in pl. 6, fig. 2, same locality and horizon, reg. no. V.16124b.

REMARKS. *Novantiella* must in life have been a juicy green alga, with swollen stem-cell, and thick crowded side-branches separated only by the lightest of calcification. The living *Dasycladus* itself shows such a light calcification, though situated differently (around the stem-cell). In structure *Novantiella* is no more advanced in general plan than the vermiporellid *Intermurella* previously described, though the proportions are quite different. In both, of course, it is possible that the primary branches may have divided in an outer zone of which no calcified evidence remains.

N. ordoviciana also occurs rarely in the type Craighead Limestone (V.55325b).

The name commemorates the old Celtic tribe Novantae in southern Scotland in Roman times.

Tribe **CYCLOCRINEAE** Pia, 1920

Genus ***MASTOPORA*** Eichwald 1840

REMARKS. *Mastopora*, long regarded as a problematic genus and variously allocated, was referred to the Dasycladaceae by Stolley (1896) and Pia (1927). It is an early manifestation of one of the several distinctive morphological patterns found recurrently in the Dasycladaceae, and still to be seen in the living *Bornetella*. In this pattern the side-branches radiate from the central stem-cell, and divide into smaller branches, which form expanded cup- or plate-like adjacent terminations which calcify lightly and so give a hollow thallus, whether club-shaped or subspherical.

Two species of *Mastopora* have been described from the Girvan Lower Palaeozoic; *M. parva* (Nicholson and Etheridge) Pia, a claviform Ordovician species, and *M. fava* (Salter) Stolley, subspherical and Silurian in age (Pl. 7, fig. 3). These were revised and described in some detail by Currie and Edwards (1943). A very important part of this description was the internal structure of *M. parva*, said to show sporangia or reproductive structures on the branches, subsurface to the outer cortex. This was most important, for Pia (1920), in dealing with dasyclad evolution as a whole, had postulated that such a position for reproductive structures (choristospore stage) had not evolved until the later Mesozoic. No detailed internal structure could be described for *M. fava*, by reason of the state of preservation of the material.

A revision of these two species, particularly of internal structure, was therefore undertaken by me. Preparation of new thin-sections failed to furnish new evidence for *M. parva*, so a detailed re-examination has been made of the original diagnostic section. On the other hand, important new evidence has been revealed for *M. fava*, which has some indirect bearing on *M. parva*. This is set out below under the species descriptions.

Mastopora parva (Nicholson and Etheridge) Pia

Pl. 5, fig. 2; Pl. 7, figs 1, 2; Pl. 8, figs 1–3.

DESCRIPTION. (a) *External* (abridged from Currie and Edwards). Alga club-shaped or nearly cylindrical with a tapering base and a rounded apex. A large complete specimen is 54 mm long and 10 mm wide at the broadest point; smaller individuals occur. The diameter of the hexagonal cups varies from 0·6–0·7 mm though the surface is usually too worn for accurate measurement. In surface view the small central pore which is the tubular end of the lateral branch is occasionally to be seen.

(b) *Internal.* This is based on the same thin-section figured by Currie and Edwards (1943): their text-fig. p. 236, and their plate 11, figs 8, 9. It is now re-described.

This transverse section is of a very slightly compressed individual, the outer diameter being a little over 10 mm. The central stem-cell cavity is circular and matrix-filled and is about 2·5 mm diameter, 25% or a little less of the outer diameter. From it there radiate conspicuous spoke-like primary branches. These are incompletely preserved, some origins, mid-portions and terminations being variously seen and all incomplete in a matrix of sparry and other calcite. At one point there are indications of secondary branching. This was probably general, for though it is impossible to count the exact number of primary branches at the stem-cell cavity and the number of outer hexagonal cups in which branches terminate, the number of cups is obviously much in excess of primaries, and secondary branches would be necessary to accommodate this as in other genera with similar morphology.

The outer hexagonal cups show in this section as funnel- or cup-shaped, open outwards and mostly matrix-filled (one contains a possible calcite-filled ostracod).

Currie and Edwards give maximum cup-dimensions as 1·05 mm depth and 0·75 width.

Currie and Edwards (1943, p. 237) claimed to have discovered sporangia in this slide: their account runs 'Immediately below the cups is a zone containing a more or less continuous ring of roughly circular areas, 0·6 mm in diameter. These are interpreted as sporangia. A few somewhat similar bodies lie near the central tube, but it is not absolutely certain that they are of the same nature as those forming a ring near the periphery. The presumed sporangia contain a dark green mineral associated with calcite. There are also idiomorphic quartz grains in the slide, of approximately the same size as the sporangia'.

A careful re-examination shows that all these bodies are polygonal cross-sections of crystals, sometimes corroded and often replaced by a green mineral. Although many are subperipheral several occur further in the interior, and in one case a longitudinal crystal section is seen in the plane of section. Mr P. M. Game, Department of Mineralogy, British Museum (Natural History), kindly examined them petrographically and reports that they are probably garnets partly replaced by chlorite. I see no reason to consider them as remains of sporangia: moreover, similar crystals occur in another *Mastopora* in an immature, pre-reproductive stage (see under *M. fava*).

Regrettably, I cannot agree to this specimen as a very early example of choristospore reproductive structure.

There are other claims of this kind which have been made for Palaeozoic Dasycladaceae: these are the Ordovician *Mastopora pyriformis* (Bassler) Johnson (Osgood & Fischer, 1960); the Permian *Permopora* (Elias, 1947); *Ischadites* (Kesling & Graham, 1962); and the Carboniferous *Koninckopora* (Wood, 1943).

Osgood & Fischer (1960, p. 899) record a thallus-interior 'partly filled with ovoid bodies of fine-grained calcite averaging 0·3 mm long and 0·12 mm wide, which we are inclined to accept as gametocysts. Similar bodies, generally of clear calcite are found scattered through the mud fillings and the matrix of other specimens. Of particular interest is a lens-shaped body of coarse calcite . . . within which are to be seen traces of five of the inferred gametocysts. This is interpreted as the remains of a complete gametangium'.

Elias (1947, p. 51) records one fragment of his *Permopora* 'as a fruiting stage, in all probability of *Permopora keenae* because it contains small subspherical or pyriform molds in the angles between the polygonal segments, suggestive of the occurrence of aplanosporangia in the club-shaped distal part of *Neomeris stipitata*'. The structures described are not clearly shown in his figures.

Ischadites (a Girvan example is dealt with below) is not considered a dasycladacean in the very thorough review of Rietschel (1969), and the structures interpreted as dasycladacean-reproductive by Kesling & Graham (1962, p. 950) are part of the outer calcareous plating seen in section.

In *Koninckopora* (Wood, 1943, p. 214) differences in calcification in the outer cells are explained as possible remains of former sporangia.

All these cases (except *Ischadites*) are possible remains of Palaeozoic choristospore development. None are really conclusive: all occur well before a fairly well-documented record of Mesozoic choristospore evolution. Their evaluation is further discussed in Part 3 of this paper.

Mastopora fava (Salter) Stolley

Pl. 7, fig. 3; Pl. 8, fig. 4; Pl. 9.

DESCRIPTION. (a) *External* (abridged from Currie & Edwards). Probably spheroidal or ovoid in life, usually occurs in flat or convex fragments, sometimes as much as 5 cm in length and 4 cm in width, composed of rather shallow and sharp-edged hexagonal cups; in the centre of each cup is a small circular pore . . . The diameter of the cups ranges from 1·3 mm to 3 mm. *M. fava* was apparently calcified only in the region of the cups, hence from its large size easily collapsed.

(b) *Internal.* Traces of stem-cell and branches in one specimen were figured by Currie and Edwards (1943, pl. 11, fig. 3). No clear section comparable to that discussed for *N. parva* was, however, available to these authors, and my sections have shown only fragments and debris of the outer cups and long primary branches of full-grown plants. Amongst these sections, however, is one of outstanding interest, which I interpret as remains of a young *M. fava* of only 5·5 mm diameter (the adult diameter is eight times this or more). This specimen is from the Lower Llandovery, Mulloch Hill Group, Mulloch Hill, Girvan, Ayrshire, reg. no. V.26824.

The section is strawberry-shaped, representing the slightly crushed section of a presumed originally near-spherical thallus. The maximum diameter in section is 5·46 mm. A central reniform area is interpreted as a collapsed stem-cell. The larger zone surrounding is formed of close-packed radiating club-shaped branches, seen to divide terminally into three or probably four short club-shaped secondary branches. Due to crushing and random angle of section the plane of section cuts radially one side and tangentially the other. A typical primary branch is 1·3 mm in length, with the diameter at the slim (inner) end 0·078 mm, widening slowly to a near-terminal diameter of 0·208 mm. A typical secondary branch is 0·182 mm in length, with lesser (inner) diameter of 0·039–0·056 mm, widening outwards to a diameter of 0·056–0·078 mm.

There is another fragment showing similar structure, adjacent to the main thallus.

The interpretation of this fossil is best made by analogy with the development of the living *Bornetella*, which has a somewhat similar morphology to that of *Mastopora*, both having both club-shaped and spheroid species. In the development of the spheroidal *B. capitata* (Harvey) J. Agardh, as described by Valet (1968, p. 37, pl. 9 (6)), the normal early dasyclad development of thin erect stem-cell and appearance of successive spaced verticils of lateral side-branches is succeeded by a crowding and bunching together of new developing branches to form a near-spherical head of closely-packed green primary and secondary branches, without calcification: this is reached before a diameter of 0·5 mm is achieved. Subsequent growth consists of lengthening and proportional slimming of the branches from a proportionally short central stem-cell, development of the peripheral cortex from the expanded secondaries, and cortex-calcification, to give the adult hollow thallus of about 15 mm diameter.

The Silurian fossil described above is interpreted as the *M. fava* growth-stage corresponding to the early head of *B. capitata* at the pre-0·5 mm growth-stage. It is much larger, but *M. fava* is a much larger species than *B. capitata*. The branches of the Silurian species are nonverticillate, unlike *B. capitata*, but the two have much in common.

The factors influencing the preservation of such a soft crushable and perishable structure are not known to me. Presumably, very soon after burial in the sediment, before compaction, and with only slight crushing of the plant, the juicy plant tissue was replaced by calcium carbonate out of circulating solution, possibly by osmosis. Subsequent diagenesis has stained and in part replaced the calcite, and there has also been some pyritic replacement. This kind of preservation is very rare, but the present case is not in my experience unique, for the even more delicate *Lacrymorphus perplexus*, a supposed unicellular green alga, is preserved somewhat similarly in the Kurdistan Triassic (Elliott, 1958).

Within the Silurian fossil there are occasional crystals very similar to those seen in the Ordovician *M. parva*. Both are in my view due to post-fossilization diagenesis. If the interpretation of the Silurian alga as a young *M. fava* is correct, sporangia would not have been present at this growth-stage, and this supports the rejection of the views of Currie and Edwards on the 'reproductive bodies' in *M. parva*.

Order RECEPTACULITALES Rietschel 1969

Family **RECEPTACULITACEAE** Eichwald 1860

Genus ***ISCHADITES*** Murchison 1839

Ischadites sp.

Pl. 2, fig. 2; Pl. 10.

REMARKS. The Receptaculitaceae have long been problematic fossils, sometimes referred (amongst many other groups) to the Dasycladaceae (e.g. Kesling and Graham 1962). They have recently been reviewed in great detail by Rietschel (1969) who shows decisively their differences from Dasycladaceae, in spite of some similarities. He concludes, however, that they are green algae, and erects the order Receptaculitales for this wholly extinct group.

In this connection the living non-calcified *Dictyosphaeria* (Order Siphonocladales, Family Valoniaceae) is worthy of comparison. The thallus forms a hollow cushion of adpressed polygonal vesicles, and it eventually ruptures to form an irregular membrane. If such a plant grew more regularly (*Ischadites* is almost mathematical in the orientation of its plates, similar patterns occurring higher in the plant kingdom in some cacti) and if the alga calcified, so precluding normal rupture, then a similar structure to that seen in the fossil *Ischadites* might be preserved. This is not to postulate close relationship, for *Ischadites* has a characteristic and peculiar plate-pattern. There are however morphological resemblances and it does seem likely that it is an extinct green alga.

In the material examined a large thin-section shows a random section of an undoubted *Ischadites*, with characteristic plate-structure; this is from the Upper Ordovician of Balclatchie, Ayrshire, Mrs Robert Gray Collection, reg. no. V.15445a.

Part III

THE EVOLUTION OF REPRODUCTIVE STRUCTURES OR ORGANS IN THE DASYCLADALES

Introduction. The dasycladacean flora described above from the Scottish Lower Palaeozoic is of interest in the relative primitiveness of the inferred position of the reproductive structures, in spite of the variety of form of thallus, especially that of the elaborate *Mastopora.* The supposed visible reproductive bodies of *M. fava* are shown to be inorganic. Presumably its true reproductive structures were non-calcified and located within the stem-cell, the "endospore" stage of Pia's terminology (Pia, 1920), as were those of the other simpler genera described.

Patterns of dasycladacean reproductive structure. In the Dasycladaceae the reproductive structures, as preserved in the fossils, yield little or no direct evidence of the sexual mechanisms involved, thus differing from the structures seen in fossil Melobesioids (Lemoine, 1961, 1971) or Chaetangiaceae (Elliott 1961). Conventionally known as sporangia, they are interpreted by analogy with what is known of living Dasycladaceae (cf. Valet 1969). Frequently resting cysts are formed which only germinate after breakup of the calcareous structure of the plant, whether before regeneration or after death, and many fossil genera must have been similar. The living *Dasycladus* itself is an exception to this, releasing gametes direct, as its calcification is confined to the exterior of the stem-cell. This is probably a secondary adaptation. The existence of *Chlorocladus*, a 'cysted *Dasycladus*' which has long been doubtful, has recently been confirmed by Valet (1969).

Pia regarded the primitive condition as that in which the sporangia were located within the thick central stem-cell; his endospore stage. For many genera this can only be inferred (though reasonably so) from the thick stem-cell and thin side-branches. Direct evidence of this condition occurs in the Triassic species *Diplopora phanerospongia* Pia and *D. tubispora* Ott, where calcified sporangia occur visibly within the stem-cell cavity, itself inside the elaborate calcified external branch-structure. Other apparently problematic fossils e.g. *Atractyliopsis* (Carboniferous and Permian) and *Aciculella* (Permian and Triassic), are interpreted as remains of dasycladaceans which calcified only their endospores or between them, so giving rise to cylindrical tubes or rods of hollow spheres, with no calcified trace of the branch-systems (Elliott, 1971a). Endospore genera are characteristic of the Palaeozoic and do not survive the Mesozoic so far as known. Endospory however has been observed as an abnormality in certain cultured living *Acetabularia* (Valet, 1968, 65–66).

A more advanced evolutionary stage of this sporangial migration within the plant is the cladospore, where the sporangia are located within thick swollen side-branches. This stage appears in the Permian (e.g. *Goniolinopsis*) is especially characteristic of the Mesozoic, and survives into the Palaeocene. In many genera the swollen primaries and diminished stem-cell diameter are taken as indirect evidence of cladospory. But there are more definite examples. *Triploporella* (Jurassic-

Cretaceous) shows swollen primaries filled with discrete sporangia, and the swollen spherical branches of *Cylindroporella* (Jurassic-Cretaceous) are obviously sporangial since they occur in verticils alternating with those of thin normal branches. The change from endospory to cladospory took place in different stocks at different times. In the Alpine Triassic *Diplopora annulata* Schäfhautl a dimorphism between presumed endospore and cladospore individuals is to be seen. The complicated explanations, both biological and taxonomic, of this by Pia (1920), have been simplified taxonomically by Herak (1957).

Another modification of the cladospore stage is the fusion of the swollen primary-branch verticils into calcified cups, as seen in *Clypeina s.l.* (Permian to Mid-Tertiary).

This genus has often been classified with the choristospore *Acetabularia* and *Acicularia*, showing similar terminal discs, usually single. But *Clypeina* appears before the choristospores, and is best interpreted as a modified cladospore (Elliott 1968, text-fig. 16).

In the third, last and most advanced stage of evolutionary sporangial migration within the plant, the choristospore stage, the sporangia are borne as separate structures upon the branch-system. This stage appears in the Mesozoic, is especially characteristic of the Tertiary and is seen in all living Dasycladaceae.

The position of the sporangia in living choristospores is variable as between different genera. In *Bornetella* they occur along the primary branches; in *Dasycladus*, *Cymopolia*, and *Neomeris* in the junctions of primary and secondary branches, in *Batophora* adjacent to the ends of both primary and secondary branches. In *Acetabularia* and *Acicularia* the reproductive structures are fused into terminal discs or cups, and a halfway stage to this survives in *Halicoryne*. Even more than the endospore-cladospore transition, the evolution from cladospore to choristospore took place in different stocks at different times in different ways. An early example of this may be seen in the Lower Jurassic *Eodasycladus ogilviae* (Cros and Lemoine 1966). Here, verticils show primary branches each dividing into secondaries, and they in turn into tertiaries. In some examples, one of the secondaries in each branch-system is swollen into a spherical sporangium, not giving rise to tertiaries but enveloped by the other dividing, secondaries. This is a specialization of cladospory which is transitional to a true choristospore.

A second, different transition is seen in the Upper Cretaceous *Cymopolia eochoristosporica* (Elliott 1968). Here swollen cladospore primary branches divide into a typical cymopoliform cluster of four thin secondaries with a small central spherical sporangium. The species shows in fact the evolutionary origin of the normal cymopoliform branch-structure seen in Tertiary and living species of the genus. It may be interpreted as partial transfer of the sporangial contents into a new independent organ, as opposed to conversion of an existing secondary branch into a sporangium. It follows that the existing choristospore patterns of sporangial distribution are probably of diverse origin.

The specialized reproductive discs of *Acetabularia* and *Acicularia s. str.* are derived from a structure such as that seen in *Halicoryne*; already choristospore, but with the gametangium larger than the sterile branch-system. Fusion of such gametangia led to the funnel or disc structure of *Acetabularia*.

REPRODUCTIVE ONTOGENY OF THE DASYCLADACEAE. Living dasycladaceans are a relict group, with several characters setting them apart from other green algae. *Acetabularia* especially has been studied under experimental conditions, and its normal and abnormal developments are known in some detail. It is especially remarkable in being, from one point of view, a giant unicellular alga. During most of the growth of the plant the large nucleus is located within the basal holdfast or rhizoid, but on completion of the terminal cap to maximum size the nucleus divides into numerous smaller nuclei, which travel up the stalk to the cap, where they form reproductive cysts for eventual release (Hämmerling 1931, 1934, 1953; Egerod 1952; Brachet 1965).

This pattern of reproduction is believed to be fundamental to the Dasycladaceae. Although eventual sexual mechanisms are not uniform (Valet 1969, p. 637) the large basal nucleus and its break-up and dispersal are believed to be characteristic of the family.

In the development of the thallus of living Dasycladaceae an early thin stem rising from the basal portion, develops successive whorls or verticils of simple side-branches. During growth these elaborate greatly, according to the generic pattern. *Dasycladus* itself shows elaborate but consistent repeated lateral branchings: in *Bornetella* the expanded terminations of the secondaries form the calcified cortex of the hollow spherical or club-shaped plant; in *Acetabularia* most of the branches are eventually shed and the final reproductive cap is borne at the end of a long naked stem. In all three the small nuclei derived from the break-up of the large basal nucleus pass up the stem-cell when they are technically endospores, through lateral branches when they are technically cladospores, and finally into distinctive separate reproductive structures (sporangia), peripheral or terminal in position, when they are choristospores characteristic of the species.

THE COMPONENT FACTORS OF DASYCLADACEAN EVOLUTION. With the above in mind, it is possible to suggest the separate basic factors which, in combination, have brought about the rich and varied pattern of dasycladacean genera ranging from Cambrian to Recent. These are three in number, two being fundamental and the third the reason for our knowledge, such as it is, of the fossil genera which very greatly outnumber living ones.

1. The first factor is a tendency to progressive elaboration of the thallus. With growth, increased complexity of branching develops for the plant's essential photosynthesis, and this is seen in both ontogeny and phylogeny. The early dasycladaceans were probably the result of evolution from a large unicellular chlorophyte. They show a thallus consisting of an irregular stem-cell, sometimes recumbent, branching or even anastomosing, and densely set with non-verticillate simple primary side-branches. The Cambrian Dasycladaceae are known to me from published accounts such as those of Korde (1957) and not from actual specimens, but they come in this category.

In the Ordovician-Silurian, such a pattern continues, but there are innovations. *Mastopora* and its allies show the first development of the large hollow thallus with calcified outer cortex, which reappears throughout geological time and is still present in *Bornetella*. *Vermiporella* continues a primitive genus, but there is a tendency for evolution to the upright stem-cell so familiar in subsequent geological periods; e.g. the Ordovician *Intermurella* is an early example. Later in the Palaeozoic the transition to verticillate side-branches is made e.g. *Mizzia*, though the non-verticillate pattern survives into the Mesozoic e.g. *Macroporella* s. str. All subsequent Dasycladaceae are verticillate, to the present day.

Mizzia is also an example of the 'beaded thallus' pattern, more common in the Codiaceae, but seen in the living dasycladacean *Cymopolia*.

Early lateral branches are primitive and rather variable. In *Mastopora* they are already specialized. The 'diplopore' pattern of bunched branches so characteristic of the Triassic begins as early as the Devonian (Poncet 1966, 1967); this author suggests two lines of such evolution for the remainder of the Palaeozoic (one through *Velebitella* (Carboniferous) and then through a Permian diplopore) and so into the Triassic.

The 'fused reproductive disc' structure first appears in the Permian (Emberger 1958; Elliott 1968) and reappears in different guises to the present day.

Very many different patterns of branching, with primaries, secondaries, tertiaries and further branches, the branches in different proportions between different genera, mark the Mesozoic and Tertiary-Recent dasycladaceans.

The repetition of various structures in different genera at very different times has been stressed by Kochansky-Davidé and Gušić (1971).

2. The second factor is the migration of the small nuclei to peripheral positions in whatever vegetative-thallus structure has evolved. Endospore genera may be inferred from the porportionally large stem-cell of many primitive genera, and evidence is occasionally preserved calcified. A similar phenomenon is seen with cladospores (see above, pp. 368–369 for examples of these). Evidence of choristospores is very frequently preserved by direct calcification.

In reviewing *Broeckella* (Elliott 1962), a genus which shows cladospory as late as the Palaeocene, I wrote '. . . we do not clearly know the special advantage of choristosporic structures, whether a direct one in shedding elements more easily, or an indirect one in their being produced more freely and lavishly with no greater or even less strain on the metabolism of the plant, but although not properly understood it is a main trend in dasyclad evolution'.

Later, whilst still not able to answer this question, I was able to show that this major trend in dasyclad evolution, the shift of the reproductive bodies in position, had not saved them from marked decline and near-replacement by other, different, green algae in those environments suitable to both (Elliott 1968).

It can now be seen that the question I asked has no answer of the kind expected. The dasycladacean reproductive mechanism provides for peripheral dispersal of the small nuclei, and this occurs however elaborate the thallus, resulting in the fascinating range of structures detailed above. This has had no markedly beneficial effect in dasycladacean evolution, since it has not led to production of a more efficient mechanism, only to accommodation of the existing one. A comparable state of affairs is to be seen in the evolution of terebratellacean brachiopods (Elliott 1953), where the development of very elaborate calcareous brachial structures as supports for the lophophore has not resulted, so far as can be evaluated, in an improved lophophore, nor helped in arresting the decline of the group.

3. The third factor is calcification. It is not known why some algae calcify and others not, since both, calcified and non-calcified, photosynthesize together under the same conditions side by side. This is a problem for a plant biologist trained in marine biochemistry and physiology. The Dasycladaceae calcify capriciously within the family, but consistently for each genus. With very heavy calcification, a record is preserved of all structures save the outer tips of fine branchlets. Lighter calcification can vary between a thin outer sheath which leaves no evidence of the plant within, or a thin stem-cell coating which bears no evidence of the branch-system without. The importance of this lies in the fact that except under very special circumstances, such as the immature *Mastopora* described above, calcification is usually the only direct evidence of marine algae to be preserved fossil. If a naked dasycladalean has been preserved, it may be the problematic *Inopinatella* of the Silurian (Elliott 1971b).

CONCLUSIONS

It can be seen that the varied and fascinating dasycladacean taxonomic variety is the resultant of their reproductive nucleus-dispersal operating in the enlargement and elaboration of the vegetative thallus, the results preserved mostly, in part, or very little by the amount of calcification peculiar to the particular genus involved.

With this in mind, the question of the alleged Palaeozoic choristospores can be reviewed. Granted that the evidence as preserved is doubtful, and that they occur before the main cladospore-choristospore trends; are they possible?

That dasycladaceans repeated the same evolutionary trends in different families is undeniable. The tiny Bereselleae of the Carboniferous, with their own evolution of annularly-grouped zones of simple thin side-branches, yet evolved one genus (*Exvotarisella*) showing the same phenomenon of secondarily dividing thickened primary branches, familiar in the main course of dasyclad evolution (Elliott, 1970b).

Clearly it is possible that precocious reproductive structures (from an evolutionary point of view) could have developed. We see now that they would not have had much if any advantage. They must therefore be judged by the evidence, and this unfortunately is doubtful. *Mastopora parva* certainly is not choristospore; the others quoted are not indubitably convincing from the evidence as presented.

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NOTE

Due to circumstances connected with delayed publication, the important memoir of Dr. M. H. Nitecki on North American Cyclocrinitid Algae (Fieldiana Geology. vol. 21; 1970), in which *Mastopora* is merged in synonymy with *Cyclocrinites*, is not discussed in this paper.

EXPLANATION OF TEXT-FIGURE

Diagrammatic representation of selected evolutionary stages in Dasycladacean reproductive evolution. Each figure shows a portion of the stem-cell on the left, and the appropriate branch-structure on the right. Solid black = calcification; light spaced stipple = vegetative tissue; heavy close stipple = reproductive bodies (separate small calcified sporangial bodies of fig. 4 not shown stippled).

Fig. 1. *Diplopora tubispora* Ott, Triassic. Endospore reproductive bodies with calcified walls; diplopore lateral branches in outer calcification.

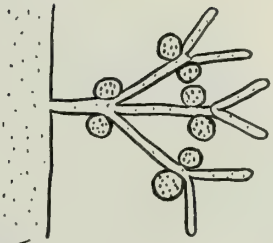
Figs 2, 3. *Diplopora annulata annulata* (Pia) Herak, with presumed endospore bodies, and *D. annulata dolomitica* (Pia) Herak, with presumed cladospore reproduction. Triassic; a possible example of endospore–cladospore change within the single species.

Fig. 4. *Triploporella* sp., Jurassic-Cretaceous. Cladospore structure; primary branches crowded with sporangial bodies.

Fig. 5. *Eodasycladus ogilviae* Cros and Lemoine, Jurassic. Adaption of one secondary branch (from several to each primary) to take reproductive bodies. This is one possible cladospore-choristospore transition.

Fig. 6. *Cymopolia eochoristosporica* Elliott, Cretaceous. Development of a small cymopoliform branch-structure of long sterile branches and central sporangium upon a large cladospore primary branch, with partial transfer of the sporangial contents. This is a second possible cladospore-choristospore transition.

Fig. 7. *Batophora oerstedii* J. Agardh, Recent. A living non-calcified choristospore dasycladacean, with reproductive bodies grouped at the junctions of primary, secondary and tertiary branches.



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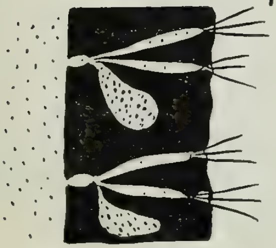

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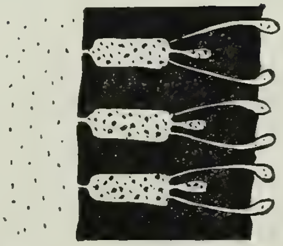

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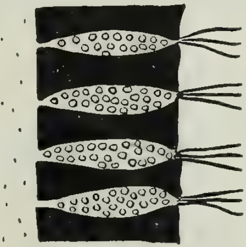

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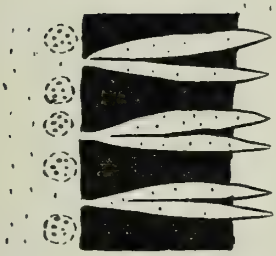

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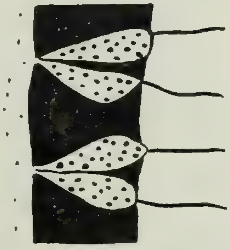

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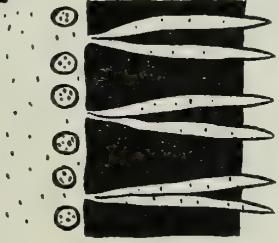

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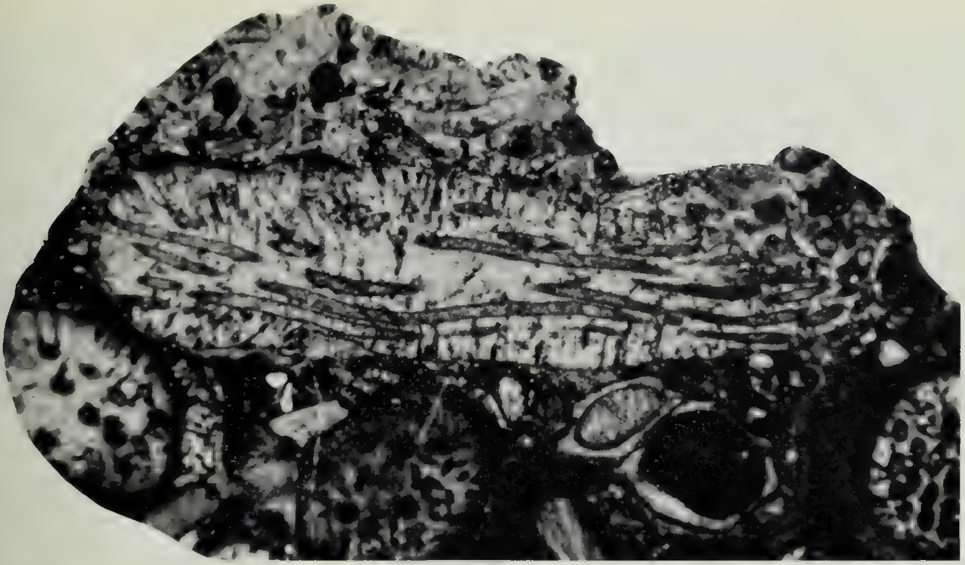
PLATE 1

Figs 1, 2. ***Dimorphosiphon rectangularis*** Høeg. Middle Ordovician: Helgoen, Lake Mjøsen, Norway. 1. Longitudinal section, ×9; V.23778. 2. Transverse sections, ×14; V.42601.



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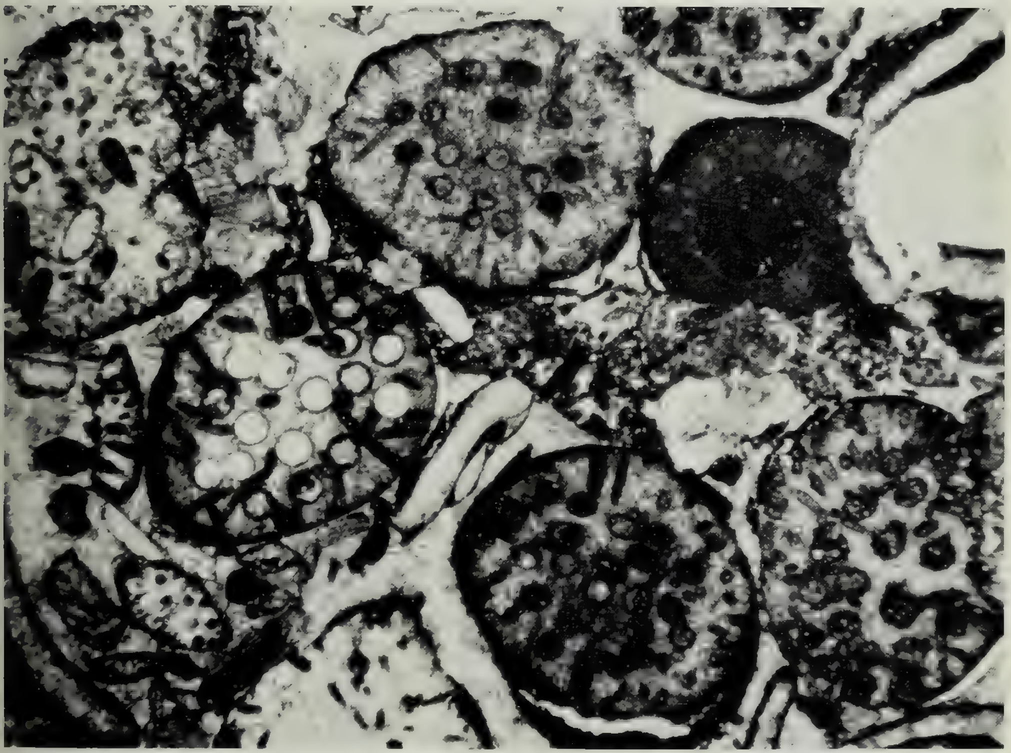

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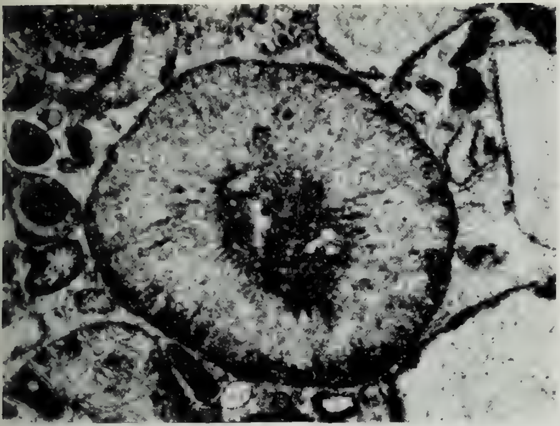
PLATE 2

FIGS 1, 2. ***Dasyporella* cf. *norvegica*** Høeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, Scotland. 1. Transverse section, ×27; V. 17067. 2. Longitudinal section, ×34; V.55325a.

FIG. 3. ***Ischadites*** sp. Oblique section of meromes (skeletal elements) in position, ×14. Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire, V.15445a.

FIGS 4, 5. ***Dimorphosiphon rectangularis*** Hoeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, V.55325a. 4. Oblique-transverse section, ×14. 5. Oblique longitudinal section, ×14.



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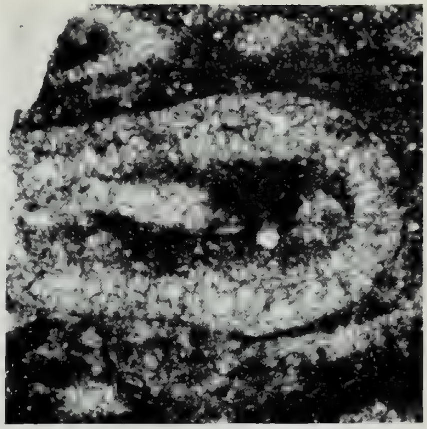

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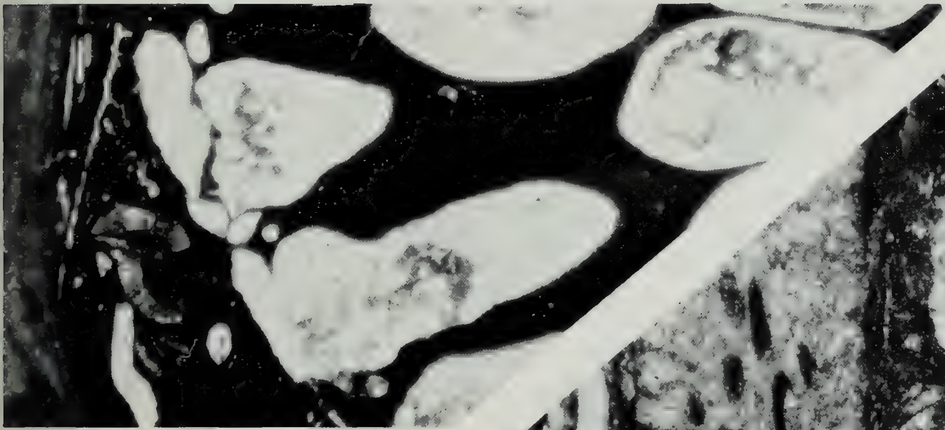

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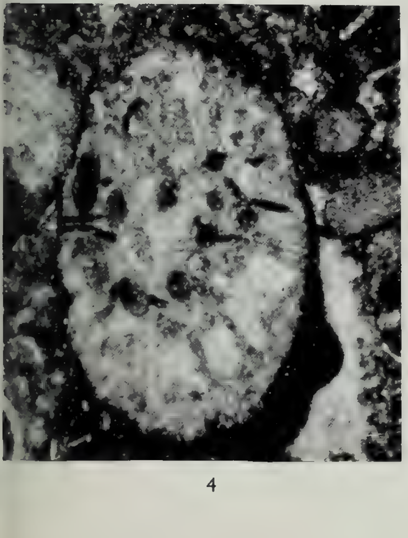

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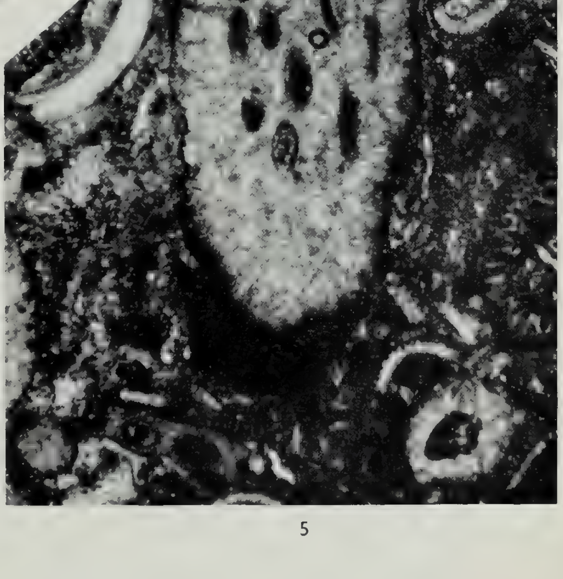

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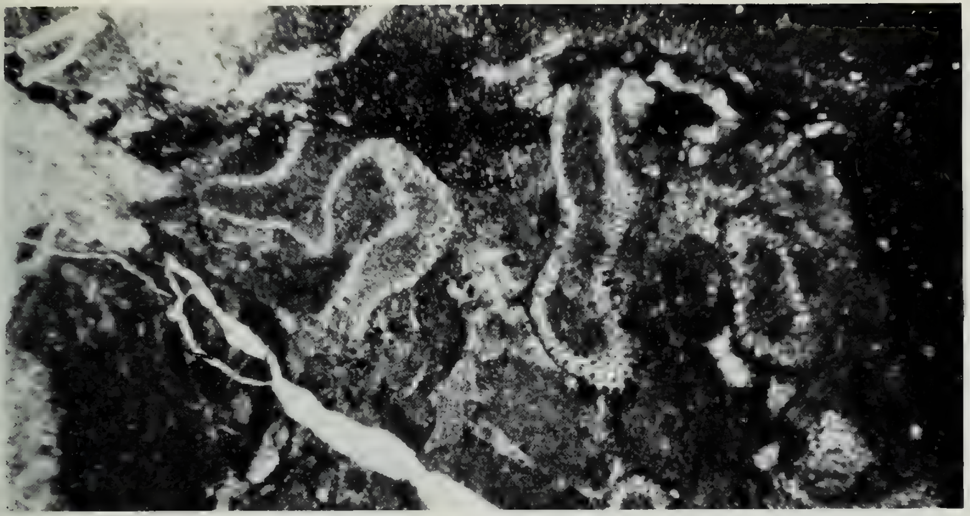
PLATE 3

FIGS 1, 2. ***Vermiporella eisenacki*** sp. nov. Middle Ordovician, Stinchar Limestone; Tramitchell Quarry, Girvan, Ayrshire, V.54162b. 1. Paratype, random sections, ×21. 2. Holotype, section of branching twisted thallus, ×27.

FIG. 3. ***Intermurella scotica*** gen. et. sp. nov. Longitudinal section, ×17. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, V.55302a.



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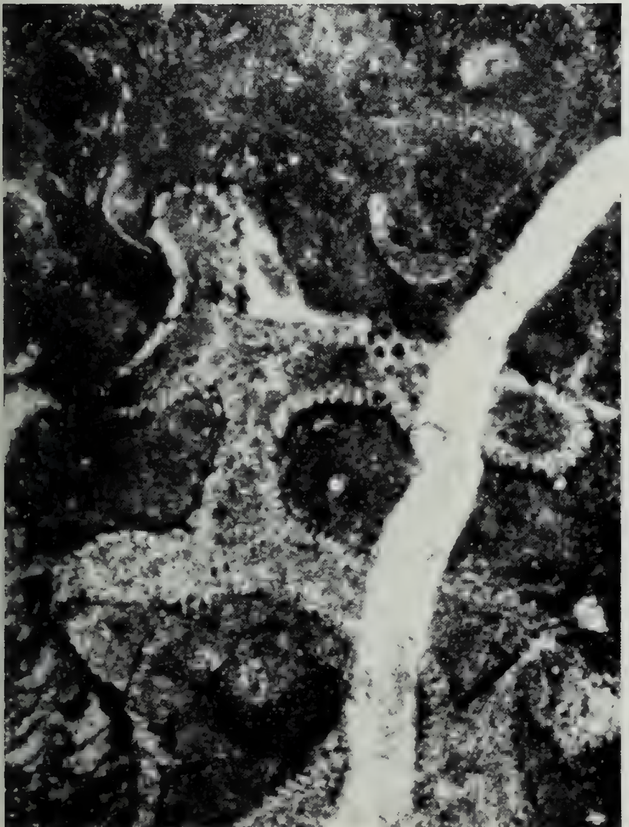

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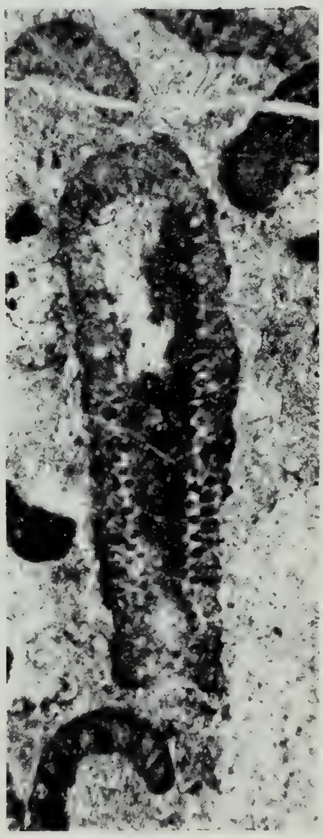

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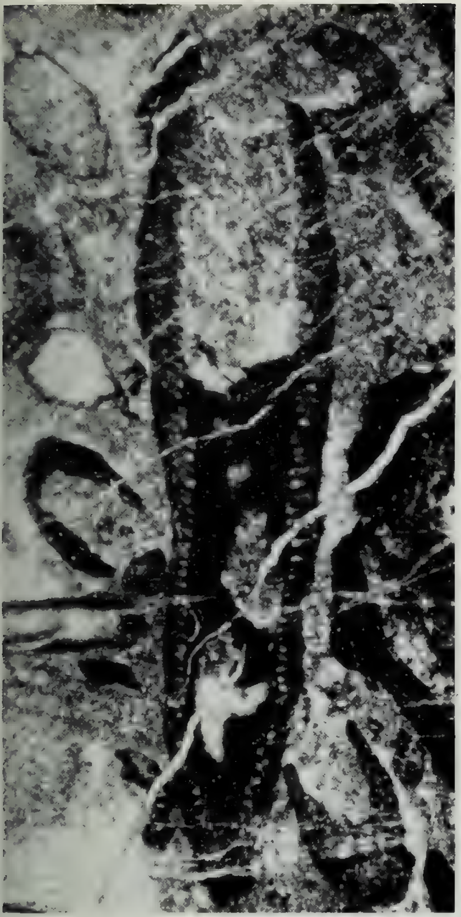
PLATE 4

Figs 1–4. ***Intermurella scotica*** gen. et. sp. nov. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire. 1. Holotype, longitudinal section, × 14; V.55302a. 2. Paratype, oblique section of curved individual, × 17; V.55302c. 3. Paratype, transverse section, × 22; V.55302b. 4. Oblique-transverse section, × 23; V.55302c.



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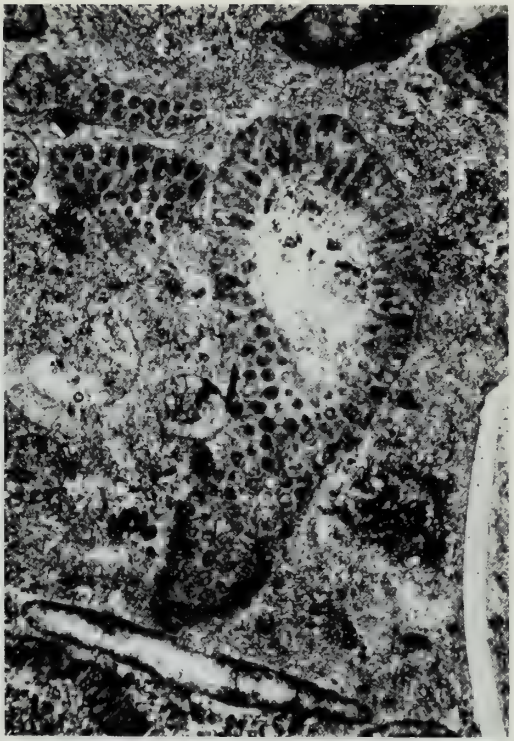

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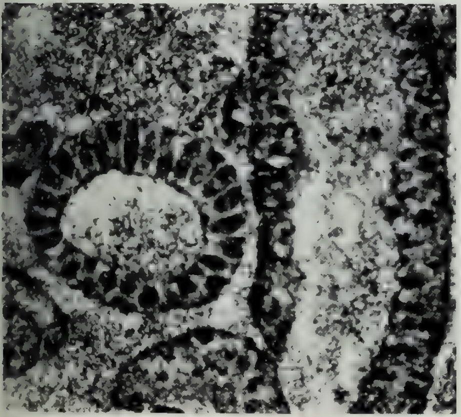

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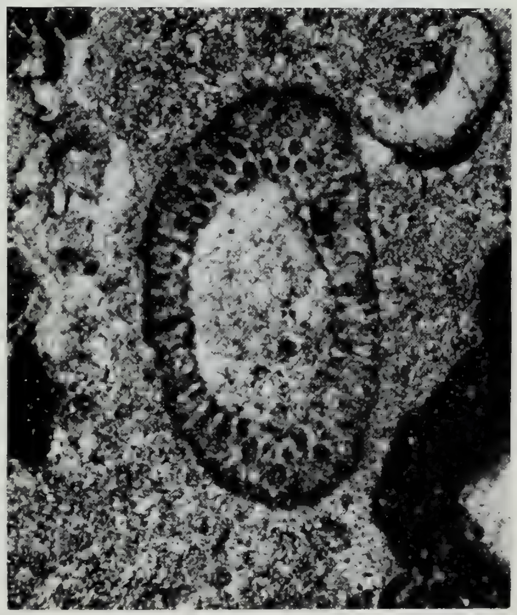

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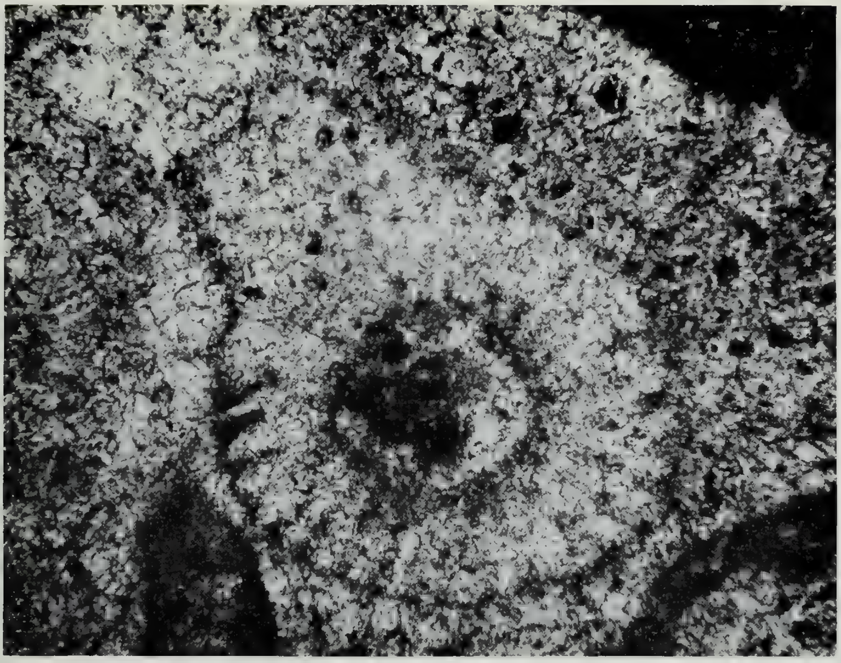
PLATE 5

FIG. 1. ***Vermiporella*** cf. ***borealis*** Hoeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire. Random Section, ×86; V.55302b.

FIG. 2. ***Mastopora parva*** (Nicholson and Etheridge) Pia. Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire. Radial primary branches interpreted as dividing into secondaries, somewhat displaced, ×45; V.16123a.

FIG. 3. ***Vermiporella*** sp. Random section, near-longitudinal, ×35. Upper Ordovician, Stinchar Limestone (Caradocian); Benan Burn, Barr, Ayrshire, V.54386a.



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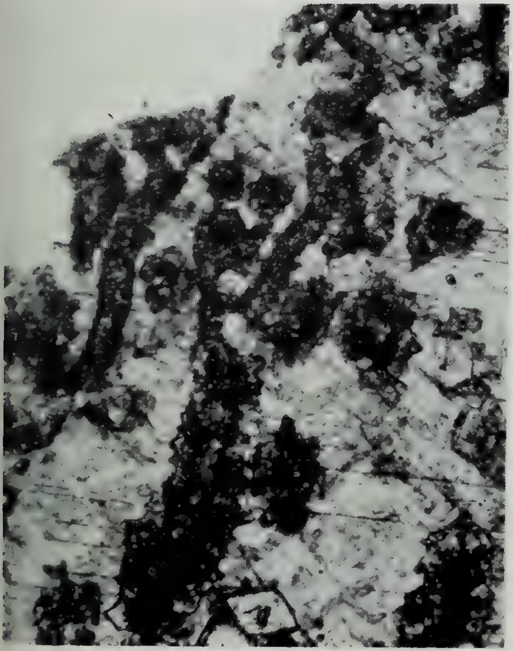

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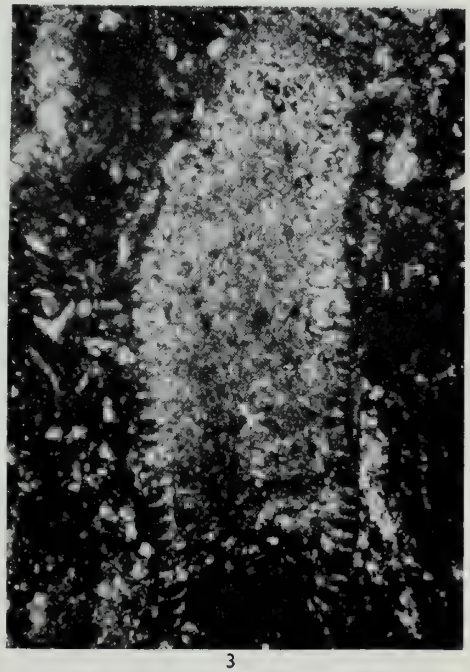

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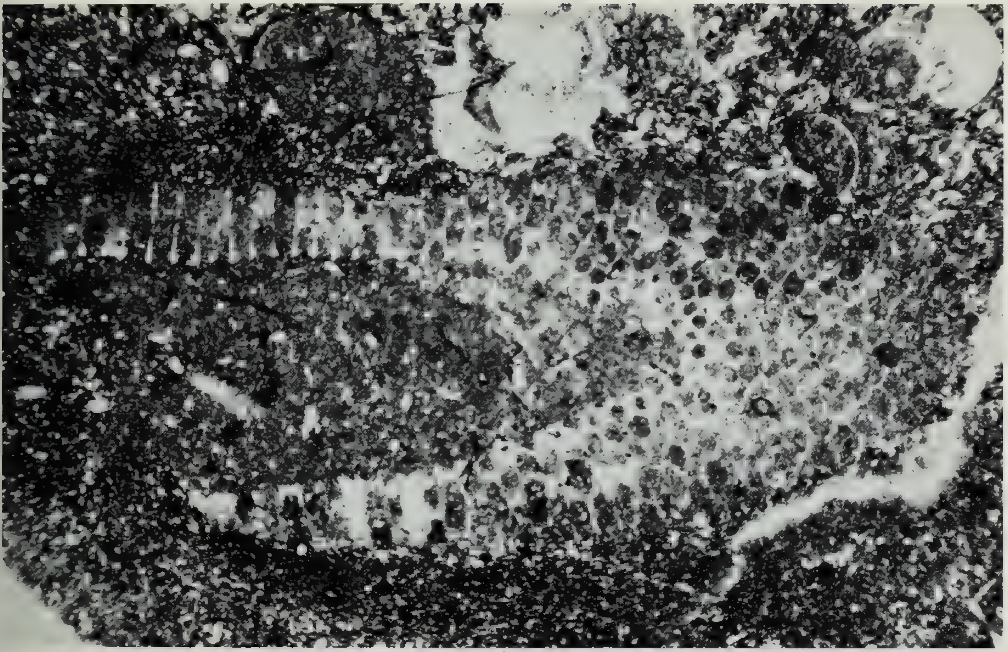
PLATE 6

FIGS 1, 2. ***Novantiella ordoviciana*** gen. et. sp. nov. Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire. 1. Holotype, oblique-longitudinal section, ×24; V.16124a. 2. Paratype, transverse section, ×30; V16124b.



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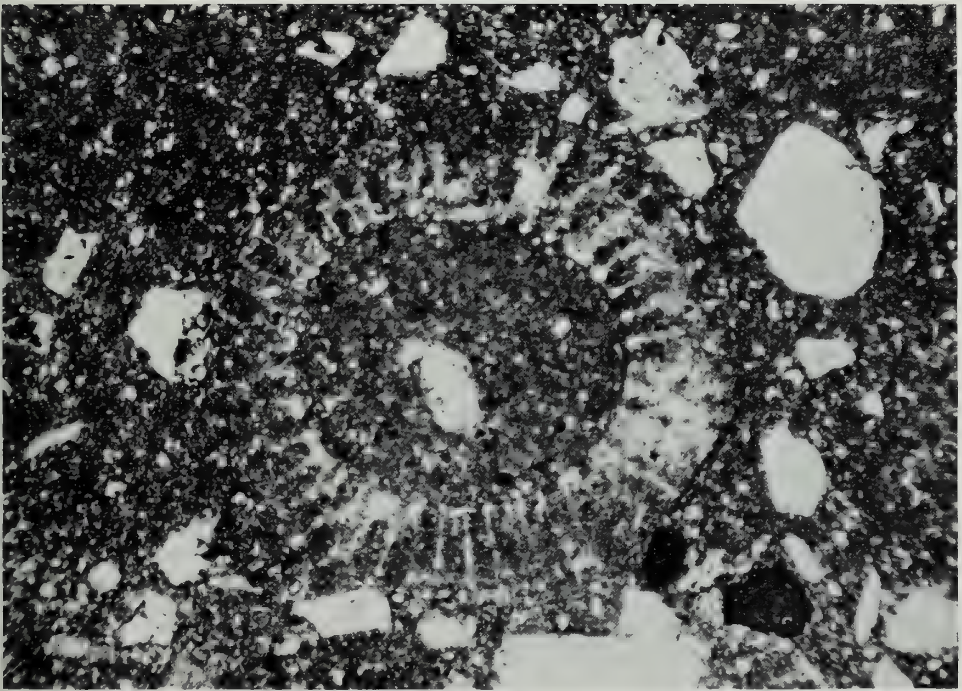

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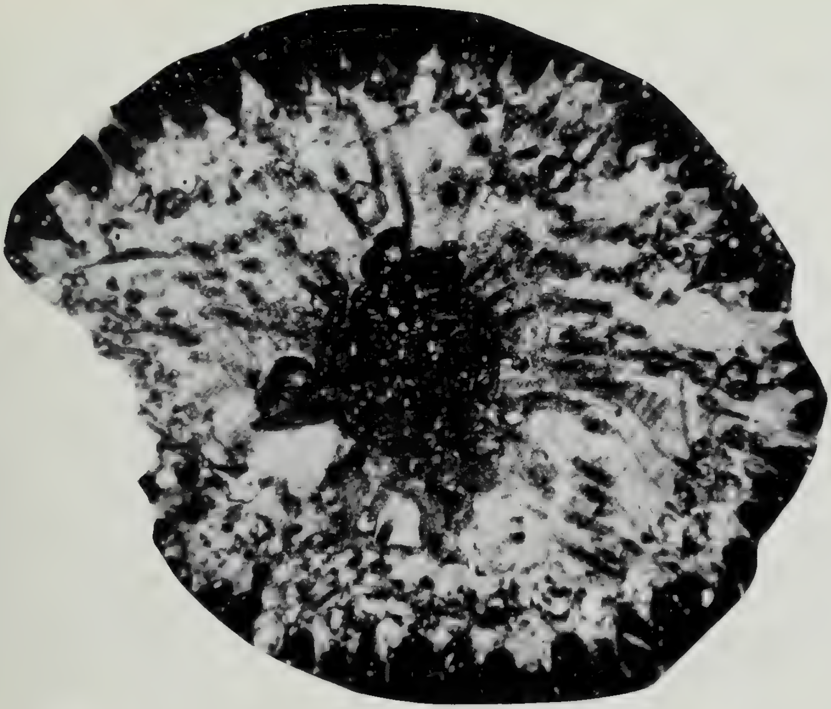
PLATE 7

FIG. 1. ***Mastopora parva*** (Nicholson and Etheridge) Pia. Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire. The unique transverse section described by Currie and Edwards (1943), ×10; V.16123a.

FIG. 2. Detail of a crystal from the interior of the *M. parva* in fig. 1; ×45.

FIG. 3. ***Mastopora fava*** (Salter) Stolley. Lower Silurian, Mulloch Hill Group (Lower Llandovery); Mulloch Hill, Girvan, Ayrshire. Uncrushed, solid, young specimen, ×4·5; V.16110.



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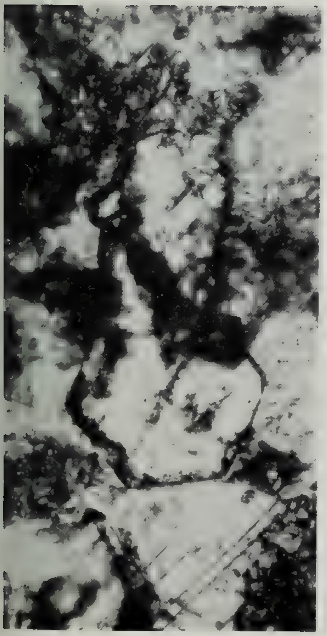

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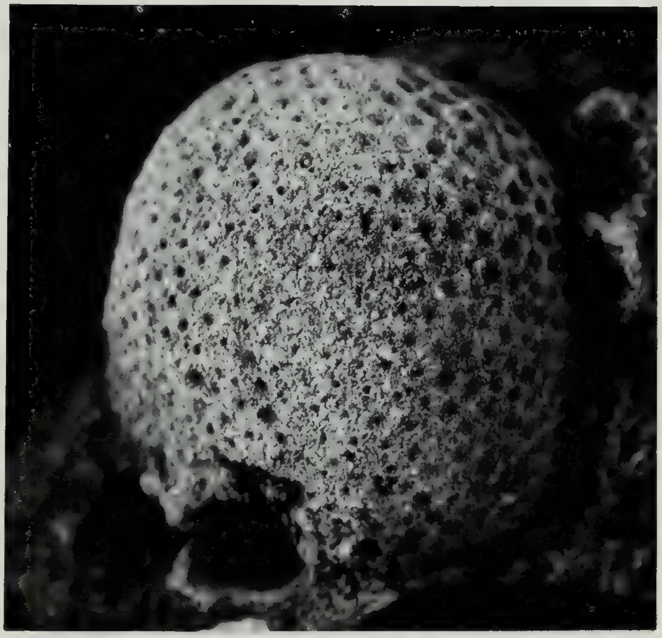

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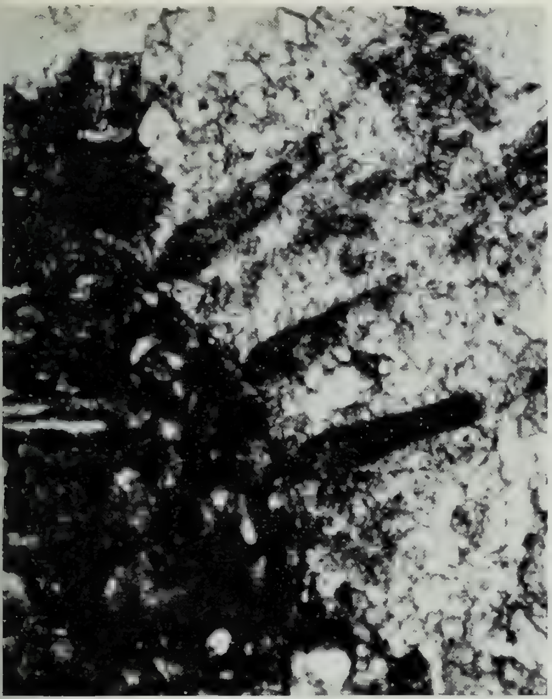
PLATE 8

FIGS 1–3. Detail from section of ***Mastopora parva*** (Nicholson and Etheridge) Pia (seen Pl. 7, fig. 1) Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire, V.16123a. 1. Primary branches radiating from central stem-cell, ×45. 2. Crystals previously interpreted as reproductive bodies, ×44. 3. Matrix-filled cups of the outer, calcified layer, and one crystal, ×45.

FIG. 4. Immature ***Mastopora fava*** (Salter) Stolley. Lower Silurian, Mulloch Hill Group, (Lower Llandovery); Mulloch Hill, Girvan, Ayrshire. Random section of moderately crushed individual showing distorted central stem-cell (originally near-circular) and adpressed, radial, uncalcified primary and secondary branches, ×14; V.26824b.



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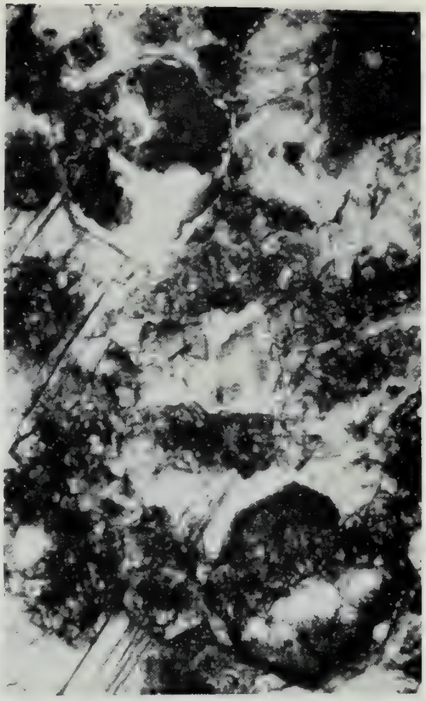

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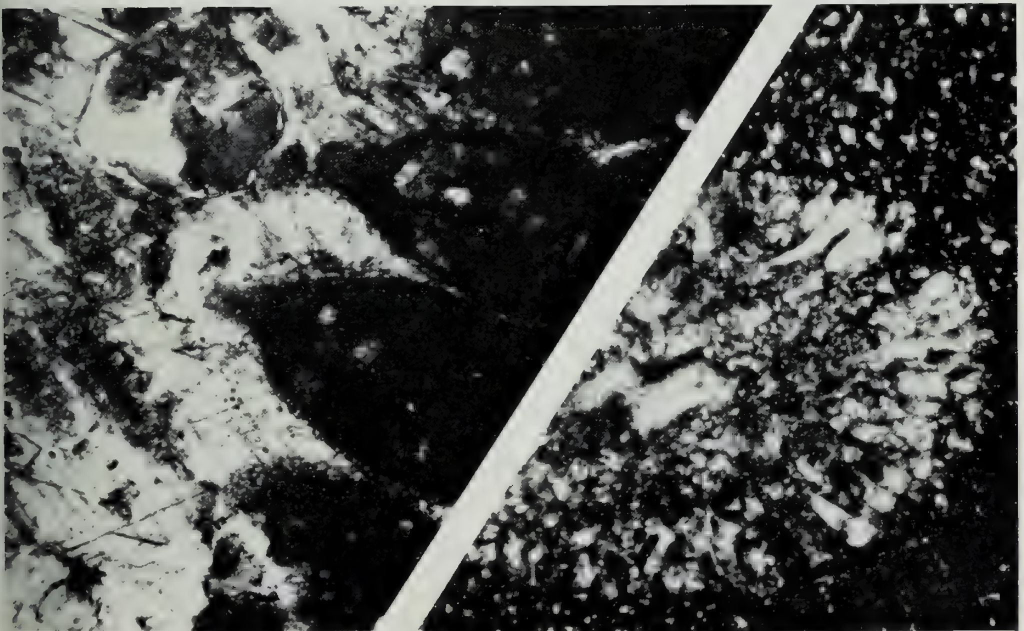

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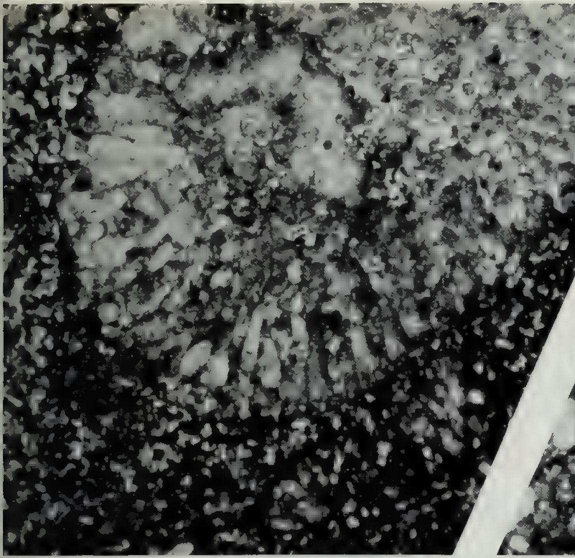
PLATE 9

FIGS 1–3. Immature ***Mastopora fava*** (Salter) Stolley. Lower Silurian, Mulloch Hill Group, (Lower Llandovery); Mulloch Hill, Girvan, Ayrshire. 1. Random section of moderately crushed individual showing distorted central stem-cell (originally near-circular) and adpressed radial, uncalcified primary and secondary branches, ×14. A different thin-section to that shown in pl. 8, fig. 4, V.26824a. 2. Detail of primary and secondary branch systems, filled with white calcite and black pyrites, from a detached fragment of the same or possibly another individual in thin-section, V.26824b; ×68. 3. Detail of primary and secondary branches, mostly calcite-filled but a little pyrites, from specimen in fig. 1 above, ×68; V.26824a.



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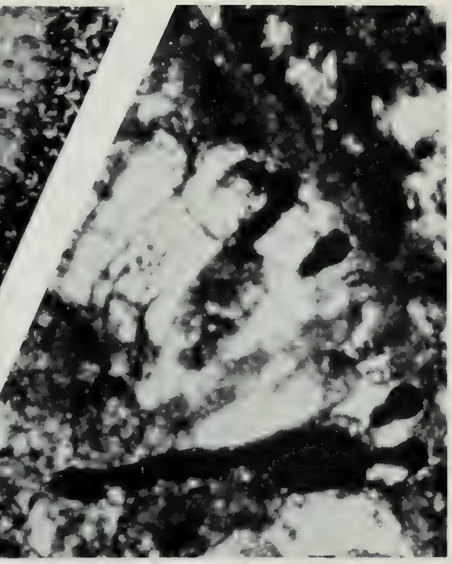

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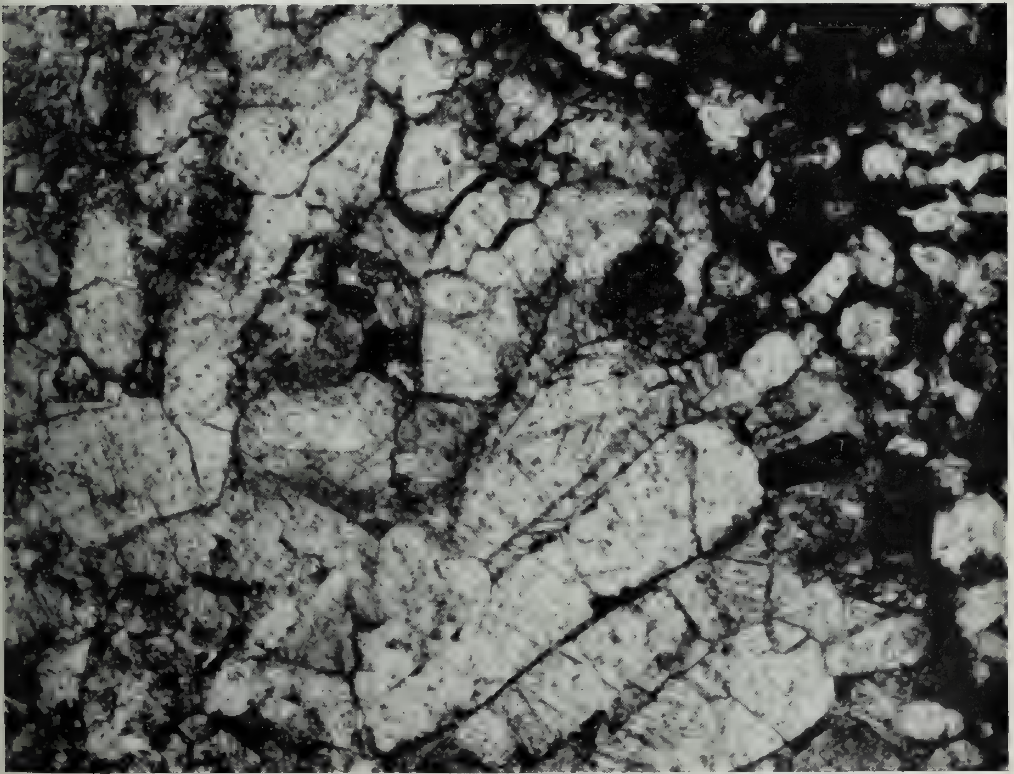

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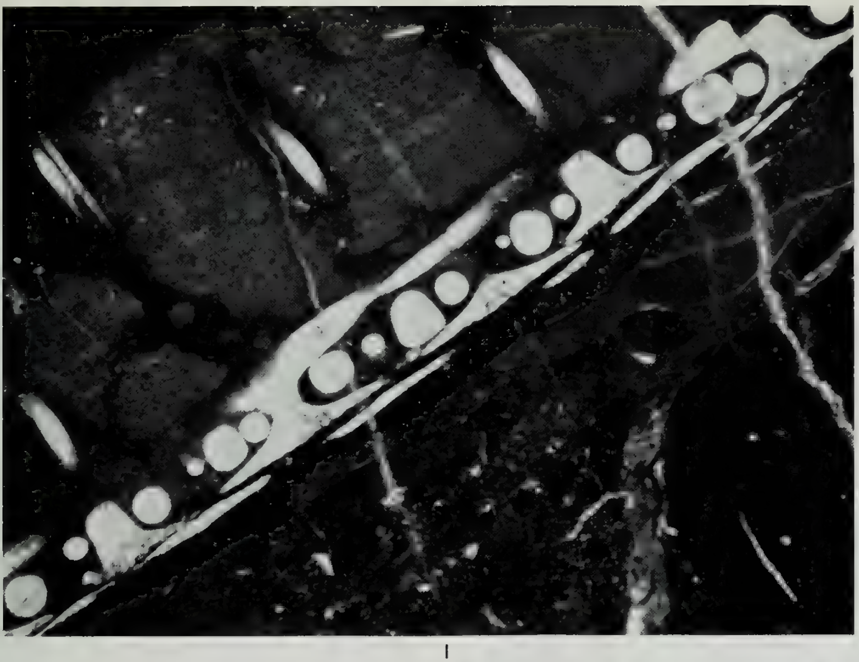
PLATE 10

FIGS 1, 2. ***Ischadites*** sp. Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire, V.15445a. 1. Vertical section of outer 'wall' or plating, showing the overlap structure of the merome outer plate and arms, sometimes misinterpreted as dasycladacean reproductive bodies; radially-set tangential cuts of the inner merome 'pillars' below, ×17. 2. Random section of displaced skeletal elements, ×14.



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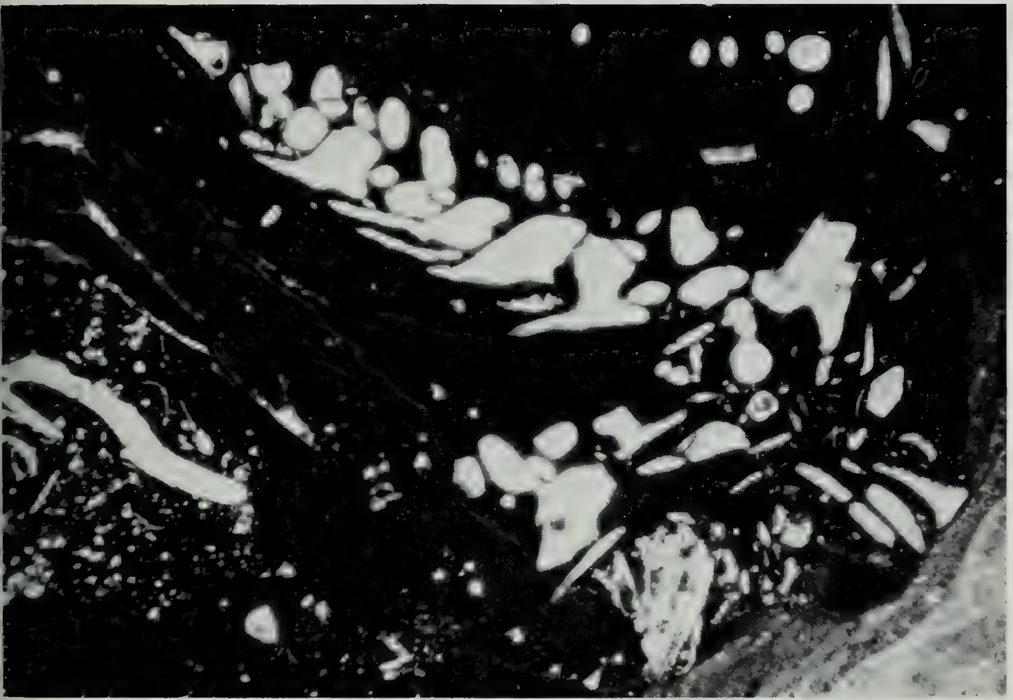

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E. I. WHITE
AND
H. A. TOOMBS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 5
LONDON: 1972

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THE BUCHANOSTEID ARTHRODIRES OF AUSTRALIA

BY
ERROL I. WHITE
AND
HARRY A. TOOMBS

Pp. 377–419; 9 *Plates*; 25 *Text-figures*

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GEOLOGY Vol. 22 No. 5
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THE BUCHANOSTEID ARTHRODIRES OF AUSTRALIA

By E. I. WHITE & H. A. TOOMBS

CONTENTS

		Page
I.	Introduction	379
II.	Systematic description	381
III.	Summary of characters	404
IV.	Relationships	407
V.	Acknowledgements	411
VI.	Localities	411
VII.	References	414
VIII.	Explanation of lettering in figures	417

SYNOPSIS

The specimens of *Buchanosteus murrumbidgeensis* collected, with two exceptions, by Harry Toombs in 1955 and 1963 are described in detail, including much of the endocranium and most of the head- and body-armour. This species is separated from the type-species as *Parabuchanosteus* and the family is placed in a new order, the *Migmatocephala*, owing to the presence in the head of dolichothoracid as well as brachythoracid characters.

I. INTRODUCTION

Some twenty years ago five fragmentary specimens of arthrodires from the Murrumbidgee Series casually collected in the Burrinjuck region of New South Wales were sent to the Dept. of Palaeontology of the British Museum (Natural History) and these proved of such interest (White 1952) that a member of the staff was sent out in 1955 to examine the area. One of us (H.A.T.) spent two months, April and May, collecting in the area, and with the generous aid given by Dr. Ida Browne and the staff of the Australian Museum Sydney, made a considerable collection. Unlike the five original specimens which had been almost completely weathered out, the new specimens were almost wholly embedded in the very tough limestone matrix. Most specimens shewed little more than a cross-section of bone, and consequently a long programme of development, largely by the acetic acid process (Toombs 1948), was necessary. However, the results exceeded expectations and in 1963, from May to July, a further visit was paid to the Murrumbidgee area and this was equally successful.

The total number of macro-specimens collected in the two visits was about 500, but of these rather less than one-half were of immediate value. There was in addition a rich assemblage of micro-fossils in the residues and of these the palaeoniscid scales have been described by Schultze (1968) and other material briefly noted by Ørvig (1969*b* : 317).

The material in these collections came from 133 localities, 51 in 1955 and 88 in 1963, with only 6 duplicated. These localities were in two discrete areas some 30 to 40 miles northwest of Canberra. Most of the specimens were found on or near the banks of the Murrumbidgee River, from a little above the new Taemas Bridge downstream to the Burrinjuck Dam, a distance of some 7 to 8 miles. A few however, came from near Wee Jasper, on the Goodradigbee River, a tributary which joins the Murrumbidgee just above the Burrinjuck Dam.

Most of the collecting was done in the Spirifer yassensis Limestone (see Text-fig. 25), but a few specimens were found to range as far up as the Crinoidal Limestone near the top of the Murrumbidgee Series, so that virtually the whole of that series is represented.

These marine beds were at one time considered to have been of lower Middle Devonian age, but more recent work on conodonts and various invertebrate groups has shewn them to be referable to the upper Lower Devonian (Siegenian-Emsian: Pedder, Jackson and Philip 1970).*

The great majority of the macrofossils were fragments of arthrodires representing at least seven genera and species, all of great interest.

Nearly all the material consists of isolated and usually broken plates and bones, and apart from head-material, in only two instances are two or more bones associated. However, in one species part of the endocranium has been preserved and it is with that species that the present paper is chiefly concerned.

This fish was originally described as a new species of the genus *Buchanosteus*, *B. murrumbidgeensis* (White 1952 : 267) on the assumption that it was congeneric with Hills' (1936) *Coccosteus osseus* which Stensiö (1945 : 8, 24) later made the type of a new genus of dolichothoracids, *Buchanosteus*. However, certain features described below seem so very distinct that we have ventured to separate this species as *Parabuchanosteus*, which with *Buchanosteus* forms the family Buchanosteidae (White 1952 : 266). Owing to the imperfection of the material of both species originally referred to *Buchanosteus*, the family was placed in the brachythoracids and the head of *B. murrumbidgeensis*, based on a narrow diagonal slice, was restored on that premise. However, the new material shows that the front of the head, with an independent rostro-pineal bone, clearly favours the dolichothoracids. Stensiö (1963 : 66 footnote, also 7, 95–110, 118, 120–123, 390) has already suggested that the *Buchanosteus* in its mixture of characters might represent a new Order intermediate between the Dolichothoraci and Brachythoraci and tentatively adds *Gemuendenaspis* (Miles 1962) to the group. The last named, like the two other supposed 'mixed' arthrodires from the Northern Hemisphere, *Euleptaspis* and *Tityosteus*, is now accepted as a true brachythoracid (Miles 1969 : 153), but the buchanosteids are placed in a separate Order, the Migmatocephala, by reason of the definiteness of the two groups of characters.

---

*Thomson & Campbell (1971 : 18) now propose to put the top beds, the Warroo and Crinoidal Limestones, back into the Eifelian—see Text-fig. 25.

II. SYSTEMATIC DESCRIPTION

DIVISION EUARTHRODIRA

Order MIGMATOCEPHALA nov.

(Gr., μιγμα,το, mixture; κεφαλή, head)

Euarthrodires shewing both well developed dolichothoracid and brachythoracid characters. Anterior part of skull-roof with separate rostro-pineal bone and broad, short preorbital plates with complete mesial contact; orbits large and directed obliquely forwards. Pattern of remainder of plates of skull-roof, of the sensory system and of the known body-plates typically brachythoracid.

At first glance the endocranium seems dolichothoracid in character, but so little is known of the brachythoracid endocranium and that only of specialized forms, that the endocranium of *Parabuchanosteus* may very well be the generalized form for both groups (see p. 406 *infra*).

Family **BUCHANOSTEIDAE** White, 1952

Diagnosis. As for Order (sole family).

Genera. *Buchanosteus* Stensiö (1945 : 8, 24) and *Parabuchanosteus* gen. nov.

Genus ***PARABUCHANOSTEUS*** nov.

Diagnosis. A buchanosteid arthrodire with spade-shaped parasphenoid, as wide as long, bearing numerous fine denticles, largest medially in front and crossed towards rear with a deep groove not quite reaching sides of plate and pierced by a pair of foramina in centre.

This diagnosis is of necessity brief and very incomplete since there is relatively little to compare it with in the unique type specimen of *Buchanosteus*(Hills 1936). The other obvious points of difference such as the concave posterior margin of the head-shield, the fine tubercular ornament and the apparent differences in the development of the central sensory canal and the posterior pit-line are likely to be at the most of specific rank; but the form of the parasphenoid, of its transverse groove and dentition are indication of more fundamental differences which cannot be established until further material is found in the type Buchan area (see Summary of Characters, p. 27).

Type species. The only species, *Buchanosteus murrumbidgeensis* White, 1952 : 267.

Parabuchanosteus murrumbidgeensis (White)

(Text-figs 1–24; Pls 1–9)

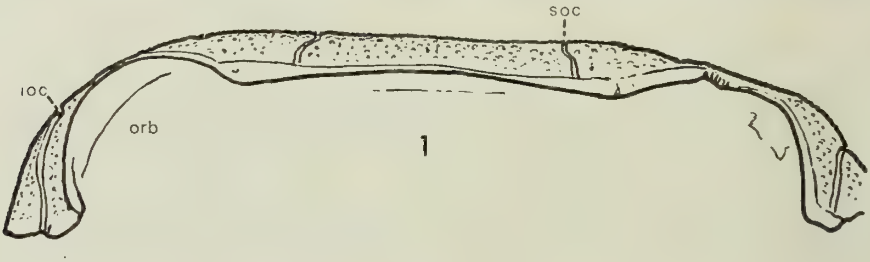
1952. *Buchanosteus murrumbidgeensis* White: 267, Text-figs 20–27; pl. 30; pl. 31, figs 1, 2.

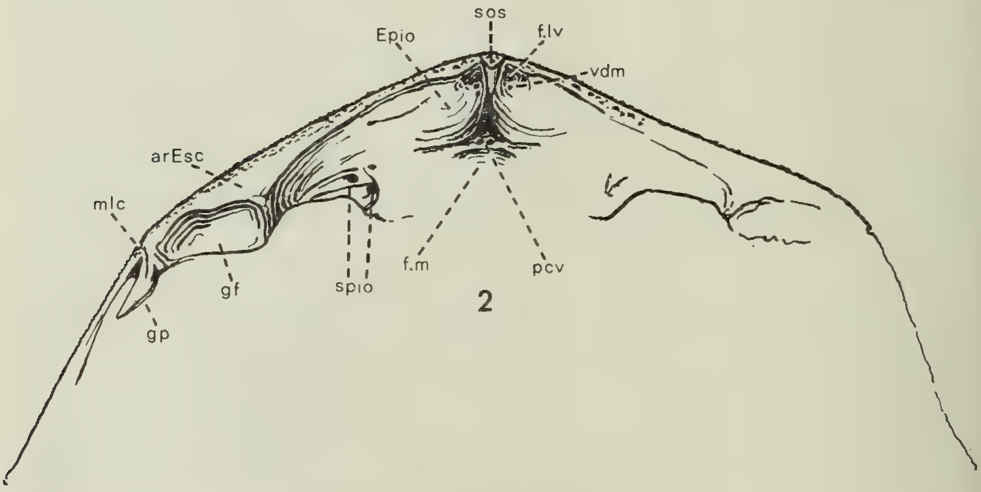
DIAGNOSIS. As for genus (sole species).

MATERIAL. The new material comprises 43 registered specimens of which 31 belong to the head-region, the remainder to the body. The head material includes 3 almost complete head-shields, one with much of the endocranium attached, and two half-heads also with the parts of the endocranium preserved. All the plates of head and body are relatively fragile.

FORMATION AND LOCALITIES. Age. Siegenian-Emsian (see foot-note p. 380). All but 11 specimens come from the Spirifer (Spinella) yassensis Limestone (see Text-fig. 25).

Those from the later beds range from the Bloomfield Limestone possibly to the Crinoidal Limestone, the most satisfactory being the left postorbital-marginal region





Parabuchanosteus murrumbidgeensis (White)

FIG. 1. Skull-roof, front view. P.48672 × $1\frac{1}{3}$.

FIG. 2. Skull-roof, back view. P.48672, with additions from P.33597, P.33683A, P.33642, P.48676. × $1\frac{1}{3}$.

of a skull-roof (P. 50367) from near the base of the Warroo Limestone at locality 1963/12. The only specimen that might have come from an older stratum is a large fragment of the skull-roof (P. 33430) collected by Mr. D. J. Cameron from the "Lower Limestone" to the NE of the Old Taemas Bridge, and its location suggests that it came from the Cavan Bluff Limestone: if so, the geological range covers most of the Murrumbidgee Series.

These 43 specimens were collected at 26 different localities scattered throughout the collecting area (see p. 411 for list).

DESCRIPTION OF SPECIMENS. THE SKULL. The skull-roof of *Parabuchanosteus* has several remarkable features. The three reasonably complete specimens, are P. 33592, P. 48672 and P. 48675, but several others add worth-while details, especially P.48676, P.33597 and P.48674 and the fragments P.33510, P.33642, P.33635, P.33683*A*.

As shewn by Stensiö in *Buchanosteus* (1963; 115, 121, 122; 1971 : 59), *Parabuchanosteus* had paired rhino-capsular bones enclosed in a discrete rostral exoskeletal capsule.

The component plates of the skull-roof are so intimately fused together that their outlines are generally obscured and no one specimen shows them all—indeed, in the third skull P.48675 (Pl. 2, fig. 3; Pl. 4), to which much of the endocranium is attached, no sutures at all can be traced. The only completely free roofing-plates are a left postorbital (P.50252) and a paranuchal (Plate 7, figs. 1, 3), and it is only a few fragments of plates from large specimens, such as two marginals (P.50382, P.50507) and a paranuchal (P.33202), that shew parts of overlapped areas, indicating that contrary to usual conditions found in vertebrates, the plates of presumably older specimens tend to be freer than in the young.

The most complete skull-roof, P.48672 (Pl. 1, fig. 1) measures in midline 97 mm from the back of the nuchal (*NU*) to the front of the pre-orbitals (*PrO*) and has a maximum breadth of 144 mm, measured over the curve at the level of the post-marginals (*PM*). This skull-roof, like the less perfect P.48675 (Pl. 2, fig. 3) is apparently very little distorted and over all is strongly convex. In front, the central area is slightly concave (Text-fig. 1) passing into a large rounded angle over the orbits so that the post-orbitals (*PtO*) are only 20°–30° from the vertical. In the posterior half (Text-fig. 2) the central part is gently convex and passes on each side into a straight or slightly concave upper plane still formed by the nuchal, and this in turn at about the nuchal-paranuchal boundary, passes into a lower, also slightly concave, plane at about 40° to the other.

The largest of the three most complete skull-roofs, P. 33592, which is much flattened and sliced across by natural micro-faults, is 108 mm in length and a little over 160 mm in maximum breadth; while the third, the most imperfect of the three skull-roofs, P.48675 (Pl. 2, fig. 3), measures approximately 100 mm along the mid-line and 162 mm (left side ×2) over the curve.

The most intriguing feature of the skull of this arthrodire is that in the pattern of the roofing-bones as far forwards as the front of the centrals (*C*, Text-fig. 3), in the very well developed articular mechanism on the paranuchals and anterior dorso-lateral plates (*ADL* Pl. 7), and in the general distribution of the sensory canal system apart from the primitive position of the occipital cross-commissure on the nuchal plate, the roof is coccosteid, as Hills (1936) clearly indicated. But in front of the centrals in the wide, very short pre-orbitals, the separate rostro-pineal bone, and in much of the form of the endocranium the skull is dolichothoracid in character.

At the back of the skull on the paranuchal plate there is a smooth triangular bevelled area reaching from near the supraoccipital spine to the outer margin of the glenoid fossa, for overriding by the extracapsular plate (*arEsc*, Text-figs 2, 3; Pl.7), which must have nearly, if not completely, filled the nuchal gap between head-shield and body-armour since there is a corresponding area on the anterior dorsolateral plate.

A similar smooth articular area for the anterior lateral plate is shared by the paranuchal and postmarginal plates (*arAL*. Text-fig. 3, Pl. 7), but not in all specimens, for in at least three specimens (Pl. 1, fig. 2; P. 33642, P.50408) this area is as strongly tuberculated as the rest of the shield.

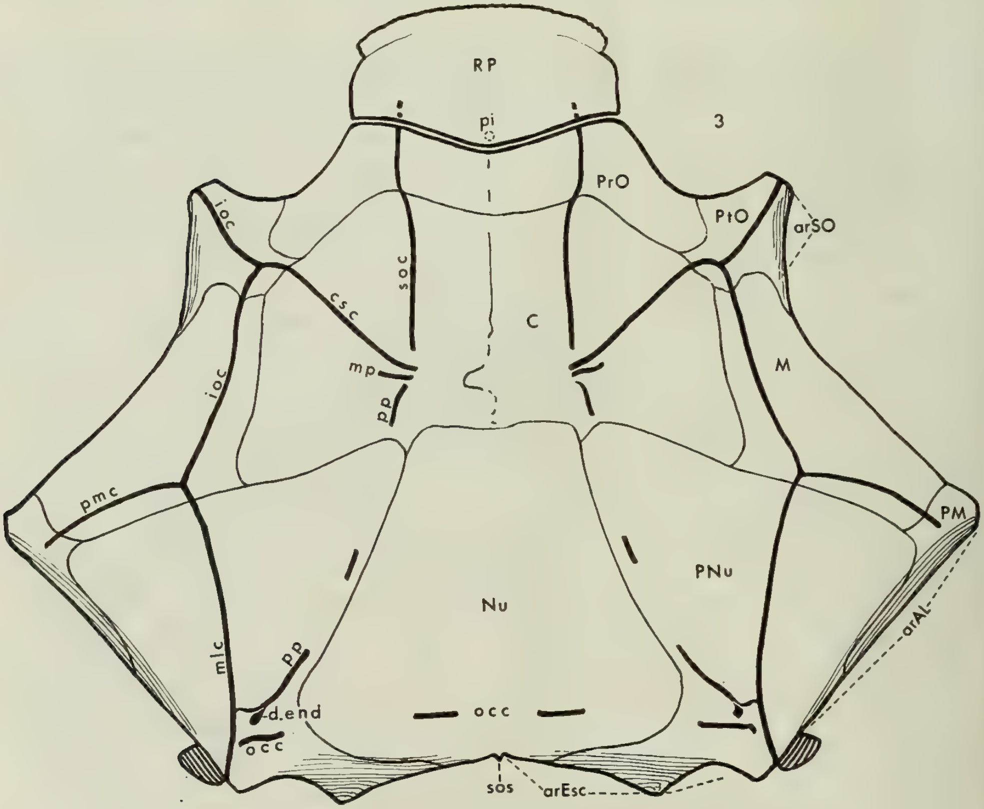


FIG. 3. *Parabuchanosteus murrumbidgeensis* (White)
Restoration of skull-roof, flattened. ×1. See Pl. 1, fig. 2.

Yet a third but small smooth area is present chiefly on the postorbital plate for the overriding of the suborbital (*arSO*, Text-fig. 3).

THE ENDOCRANIUM. The dorsal surface of the endocranium is completely fused to the skull-roof (Pl. 1, fig. 1). In only two specimens are substantial parts of the underside of the endocranium preserved: P.48675 (Pl. 2, figs 1, 2; Pl. 3, fig. 2; Pl. 4) shews it from the forepart of the parasphenoid (*Psph*) for about half the length of the skull and also most of the left side; while in P.33597 (Pl. 5, fig. 2) there is still much of the left and central posterior region in place. From these two one can deduce the general form, very low and wide with the oral surface gently concave across the roof of the mouth and also lengthwise, especially in the sub-pituitary area.

The parasphenoid is preserved in three of the specimens: P. 48672, P. 48675, P.48676, the plates showing a slight increase in size and, possibly, age in that order but also a very marked increase in decay or resorption.

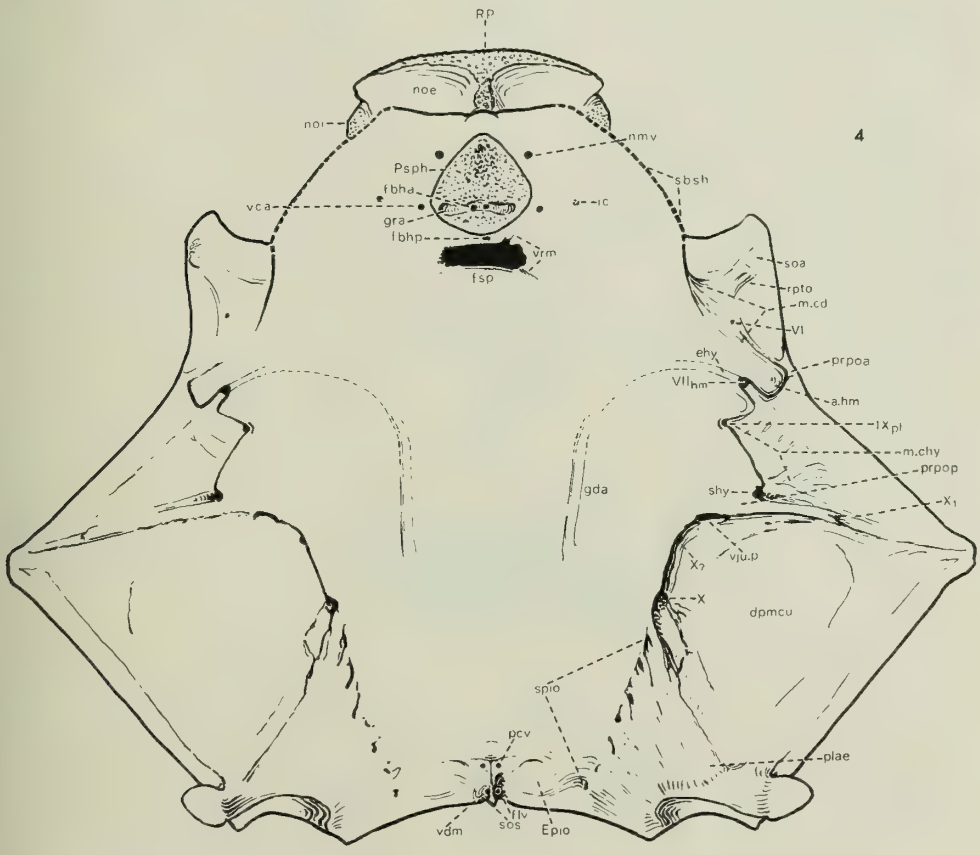

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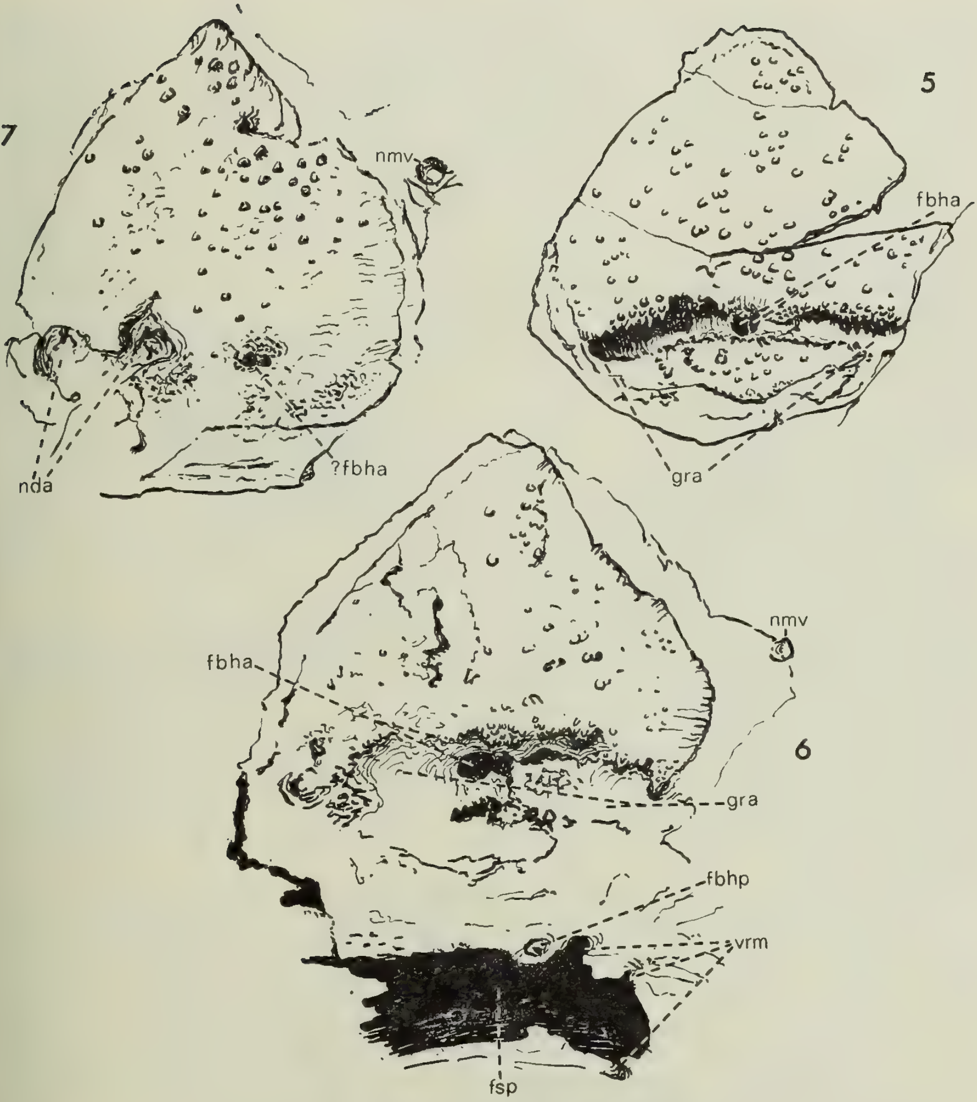
FIG. 4. *Parabuchanosteus murrumbidgeensis* (White)
Restoration of undersurface of skull, flattened. ×1. See Pl. 4.

These parasphenoids are broadly spade-shaped (Pl. 3; Text-figs 5–7), about as long as wide, measuring approximately each way 14·5 mm, 16·4 mm and 18·0 mm respectively, and so differ in shape considerably from the plate described and figured by Hills (1936: 221–2, text-figs, 4, 5) and later by Kulczycki (1956 : 106–7, pl. 1, fig. B) and Stensiö (1963 : 97–100, 121–2, text-figs 37, 44). The surface of the first and best preserved specimen (Text-fig 5; Pl. 3, fig. 1) is nearly flat and almost completely covered by numerous conical denticles, largest at the centre towards the front, and mostly with somewhat worn, rounded tips especially in the front where they were well-placed for grasping. The structure of the spongy middle layer shews through the very thin laminar outer layer between the teeth. The most marked feature of the plate is the very conspicuous groove (*gra*) which runs across the plate almost, but not quite, to each margin, deepening as it goes and slightly bowed forwards. In the centre of the groove where it is shallowest are small twin openings such as Hills identified as 'hypophysial fenestrae' and Stensiö as paired buccohypophysial foramina, (*fbha*), the right (left of figure) substantially larger than the left. But other features described by Hills are hard to reconcile with what is to be seen in our specimens. He writes of a large foramen on each side of the 'fenestrae hypophyseos'—these openings are relatively much larger in his than in our specimens—'which leads upwards into a blind sac-like pit running laterally within the bone. A smooth tract of bone surface runs between these foramina posteriorly to the fenestrae hypophyseos, and it is clear that some strand of tissue or vessel ran from one foramen to the other beneath this smooth tract'. Further he notes that 'on the nearly vertical edge of this median thickened edge' there is on each side a small ovoid foramen leading into a transverse canal which seems 'to enter the foramen leading to the sac-like pit' and 'may therefore have transmitted those parts of the internal carotid arteries external to the cavum cerebrale . . .'

The blind sac-like pits within the bone and the smooth tract connecting them presumably correspond to the large transverse groove in our first specimen, but there is no sign in any specimen of 'transverse canals' leading into it nor of the minute 'carotid foramina' in front of the 'hypophysial fenestrae'. There is no pit at the ends, but a deepening close to the margin of the plate. In the complete right side (left of fig. 1) this groove stops short of the edge, and probably on the left also. The twin foramina are not in front of the groove as in Hills' fossil but actually in it, as in *Dinichthys* cf. *pustulosus* of Kulczycki (1956, pl. 1, fig. G). Moreover, the sides of the groove bear denticles but the floor is smooth.

Dorsally the parasphenoid is expanded over its hinder part, that is the area overlying the transverse groove, into a thick-walled, dome-like outgrowth in which the ventral division of the hypophysis occupies, in young specimens at least, an unspecified part. This expansion, best seen in the following specimen, then passes into a narrow neck through which the lumen grades into the hypophysial fossa, here seen as a deep, otherwise featureless depression about twice as broad as long.

In the slightly larger, and presumably older specimen (P.48675, Text-fig. 6; Pl. 3, fig. 2) the transverse groove has been greatly widened by resorption or decay of the bone and this has left a very rough surface indeed of the cancellar layer, but the dentition, much worn in front has persisted and, although overall generally thin, is



Parabuchanosteus murrumbidgeensis (White)

FIG. 5. Rather small relatively unworn parasphenoid shewing crowded teeth and well preserved transverse groove for the 'Rachendachhypophyse' (*gra*) and twin anterior buccohypophysial foramina (*fbha*). P.48672 ×4. See Pl. 3, fig. 1.

FIG. 6. Part of roof of mouth shewing parasphenoid and subpituitary fenestra, the former with the transverse groove for the 'Rachendachhypophyse' and the surface posterior to it partly resorped. P.48675 ×4. See Pl. 3, fig. 2.

FIG. 7. Imperfect parasphenoid with oral surface completely resorped but with sparse pointed teeth re-grown in anterior region. P.48676 ×4. See Pl. 3, fig. 3.

thickly clustered along the anterior lip of the groove. In spite of this resorption the groove has been extended to break through the plate only on the left side (right of figure), but on the other side a shallow depression has been developed independently to the side of the groove. The whole surface is extremely rough and the apertures of the paired bucco-hypophysial canals (*fbha*) are much enlarged and confluent, passing immediately into a chamber above, the ventral part of the fossa hypophyseos.

A fragment of the canal of the left naso-maxillary vein (*nmv*) lies well outside the parasphenoid.

In the third specimen (P.48676, Text-fig. 7: Pl. 3, fig. 3) the parasphenoid and neighbouring vessels have been twisted out of the mid-line. Almost the whole surface of the plate has been resorped and all trace of the groove save for one or two faint depressions has disappeared. The right side (left of figures) shews a deep irregular pit which may be due either to decay or to post-mortem effects and on the left side, some distance from the centre is a pit in which is a circular perforation, and this too is unlikely to have any connexion with the living design.

The teeth are much sparser than even in the last specimen. The large very worn teeth have persisted in front, but here and there elsewhere small sharp teeth give the impression of being regenerated rather than residual, especially as one occurs within the 'crater' of the perforation mentioned above.

The persistence of the anterior part of this plate in both second and third specimens at the time the rest of the plate has undergone profound alteration is most puzzling, particularly in relation to the transverse groove, which in any case seems unlikely in its form and impersistence, let alone its nearness to the surface of a biting plate, to have housed a blood vessel, especially such an important one as Stensiö's (1963 : 122, text-fig. 44) 'Sub-hypophysial transverse anastomosis of the internal carotid arteries'. If such an anastomosis were present, one would expect it to pass above the parasphenoid, as in *Tapinosteus* and *Pholidosteus* (Stensiö 1963 : 211, text-figs. 63, *gr.a.com.;* 68*B*, 69*B*, *a,com.*).

These objections apply with still greater force to Kulczycki's suggestion that the small central foramina are those of the internal carotids themselves (1956 : 107–9, pl. 1, *c.aci*). Another suggestion that has been put forward is that the true homologue of the transverse groove, whether complete or divided (*cf.* Miles & Westoll 1968 text-fig. 18*a*, *gr.a.com*) is the 'prespiracular groove' of *Glyptolepis* (Jarvik 1954 : 39, text-fig. 20, *gr.psp*). However, Kulczycki has already repudiated this idea on account of the supposed lack of denticles in the groove in arthrodires and the presence of the 'bone-bridge'. Indeed, the smooth broad shape etc. of the under face of the endocranium bears little resemblance to that in the crossopterygian.

Attention may be more profitably directed to the hypophysis in chimaeroids, in which there is a marked extra-cranial (oral) component, the 'Rachendachhypophyse'. In small specimens of *Hydrolagus* it is "in the form of symmetrical tubular structure in cross-section' but in the adult it is 'three times as large as that of immature animals' and 'a massive compact organ' (Sathyanesan 1965: 414–7, figs 1–12).

Meurling (1967 : 89, 102) in his study of *Chimaera* discusses the possible homologies of the Rachendachhypophyse, either with the ventral lobe of the pituitary of elasmobranchs, or as an outgrowth or remnant of the hypophysial stalk. The latter is the more relevant to our purpose. The depression in the cranial base which lodges it is, according to Allis (1917 : 115), a remnant of the hypophysial fenestra, so marked a feature in some arthrodires (Stensiö 1963 : 137, figs 14, 15, 36*c*, 47*a* etc), and this is still open in embryos and, importantly, sometimes in young specimens (Fujita 1963).

There are then features which provide grounds for suggesting that the subhypophysial transverse grooves in the parasphenoid of *Parabuchanosteus* may have housed an organ comparable to the Rachendachhypophyse in living chimaeroids, such as its position relative to the hypophysis and to skull base and mouth, and its

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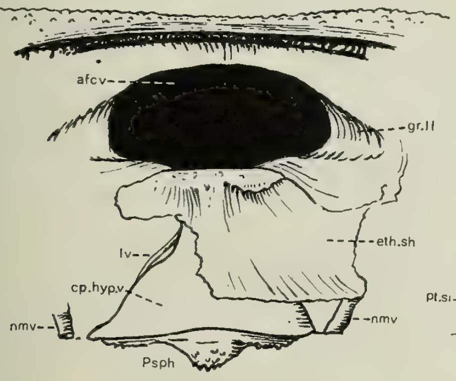
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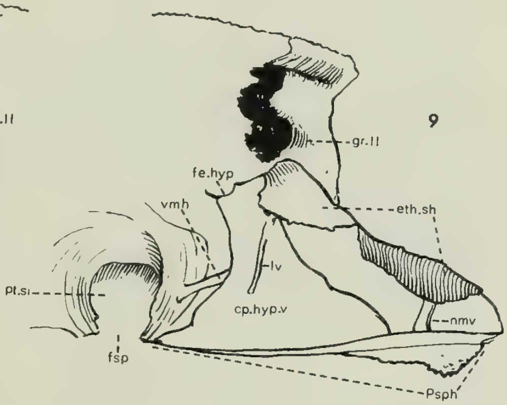
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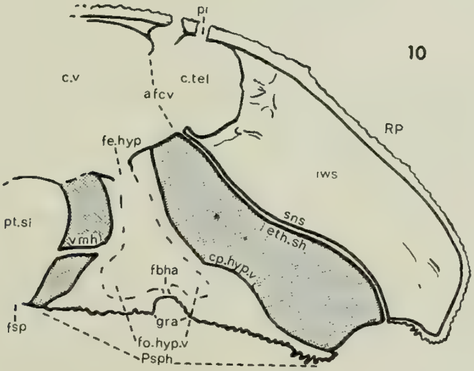
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Parabuchanosteus murrumbidgeensis (White)

FIG. 8. Direct front view of imperfect post-ethmoid part of skull, partly restored. Based largely on P.48675. ×2 approx. See Pl. 2, fig. 2.

FIG. 9. Slightly oblique right lateral view of same with part of side wall removed. ×2 approx.

FIG. 10. Diagrammatic median longitudinal section through rostropineal bone and anterior post-ethmoid region. ×2 approx.

twinned form. Its broad transverse form is to some extent paralleled by the 'posterior transverse part of the hypophysis' which Stensiö (1963 : 95 text-fig. 36) postulated as occupying the broadest, posterior part of the bucco-hypophysial foramen 'corresponding to the broad, transverse hindmost part of the embryonic hypophysis of the Selachians'. That such an organ should in older specimens disappear with the general atrophy of the parasphenoid is curious, but we do not yet know fully the function of this part of the hypophysis, and in any case its disappearance is not so remarkable as that of an artery would have been (*cf.* Stensiö 1963 : 97 text-fig. 37D).

In a later brachythoracid, *Tapinosteus* (Stensiö 1963, *c.t.* text-figs. 48, 71, etc.) this transverse groove is reduced to a pair of canals 'terminating in interior of the parasphenoid (without any opening into the fossa hypophyseos)' on either side of the pair of very small buccohypophysial canals.

The other remarkable feature shewn on the broad ventral surface of the endocranium is the large transverse fenestra immediately behind the parasphenoid. This underlies a very large pituitary sinus (*fsp;pt.si.*, Text-figs 9–11) precisely in the position in '*C. osseus*' of Stensiö's 'possible subpituitary fossa', 'groove or canal for pituitary vein' and 'canal for pituitary vein and for the rectus externus muscle of the eye' (1963 : 121–2, *f.sbp.*, *gr.v.pit.*, *c.v.pit.*, see also pp. 48, 56–62, 70, text-figs 14, 15, 20*D–F*, 25, 41, 48*B*, 49*C*, etc.). The supposed differences between the two forms may be partly due to crushing in Stensiö's material with the possibility that in *Kujdanowiaspis* and in the other forms restored after it the median part of the pituitary vein was in fact not 'situated underneath the endocranium', but ran through it. This subpituitary fenestra is only preserved in the one specimen P.48675 (Text figs 4, 6, 9–11, Pl. 2, fig. 1; Pl. 3, fig. 2) and in that only the left side (right of figures) is complete, and this shews that at least two vessels (*vrm.*) entered at the margin of the fenestra, which from the tributary markings on the bone were veins draining from the roof of the mouth into the pituitary sinus.

On each side of the parasphenoid near the anterior end is a conspicuous, nearly vertical canal (*nmv*, Text-figs 4, 6–9, see also Pl. 2, fig. 2, Pl. 3, figs 2, 3; Pl. 4) running up from the roof of the mouth, which was possibly for the naso-maxillary vein, while further behind is the foramen of the anterior cerebral vein (*vca.*). Little further out from this must have been the internal carotids, but the area is not preserved.

The only other feature shewn on the remnant preserved of the general surface of the endocranium is the faint impression of part of the left dorsal aorta (*gda*).

The left (right of figures) marginal area is largely intact in P. 48675 (Text-fig. 4; Pl. 4) behind the level of the post-orbital (*PtO*), but the suborbital shelf and, if any, the ectethmoid process are missing in all specimens.

The first feature of interest is the ridge under the postorbital plate (*rpto*) at the distal end of which is the articular head for the suborbital plate (*soa*). This ridge is the 'anterior postorbital process' in Stensiö's (1963 : 120, text-fig. 44, *pr.poa*) restoration of *Buchanosteus* and between this and the true anterior postorbital process (*prpoa*) is the area for the dorsal attachment of the *m. constrictor dorsalis* (levator palatoquadrati; *m.cd* Text-fig. 4, see Edgeworth 1935 : 46, figs. 110, 111, etc.) and a foramen possibly for the abducens nerve (VI). The end of the process is always unossified and presumably bore a cartilaginous area for the articulation of the hyomandibula (*a.hm*). Immediately behind is a deep invagination leading to the canal for the hyomandibular branch of the facialis nerve (*VIIhm*), and below this the groove for the efferent hyoid artery (*ehy*). A smaller invagination shortly behind is possibly for the exit of the pharyngeal branch of the glossopharangeal nerve (*IXph*). Between this and the posterior postorbital process (*prpop*) the floor of the endocranium projects, so that the side is concave and is marked by a series of parallel ridges which are continued on to the underside of the skull-roof (*m.chy*) being the attachment scars of the upper side of the *m. constrictor hyoideus* (Edgeworth 1935 : 98, fig. 110, etc) and possibly also for the *m. adductor mandibulae*. Other details of this region may be seen in the much fractured right side (Text-fig. 11; Pl. 2, fig. 1) which gives a lateral view of parts of some of the canals inside the endocranium (*cf.* Stensiö 1963, text-fig. 28). Conspicuous in front is the exit of the efferent pseudobranchial artery (*psba*) which passes into a large anterior myodome, and shortly behind that is the exit of the oculomotor nerve (III) with possibly a second myodome for the superior oblique eye-muscle. Immediately below is the relatively enormous pituitary sinus (*pt.si*) above the sub-pituitary fenestra (*fsp*; see also Pl. 2, fig. 2 and Text-figs. 6, 9, 10), leading into a very large posterior myodomal space (*pt.my*), for the rectus eye-muscles. This is as in Stensiö's description ot *Kujdanowiaspis* (1963 ; 55–56, 58, text-figs 14, 17, 30, 41 *et al.*) except that there the pituitary vein and the posterior part ot the *m. externus posterior* are 'extra-mural', and lie in a sub-pituitary fossa, and this fossa is also shewn in an undetermined dolichothoracid from the Lower Devonian of Spitsbergen, while *Buchanosteus* has been similarly endowed in restorations (Stensiö 1963, *f.sbp* Text-figs 15,44).

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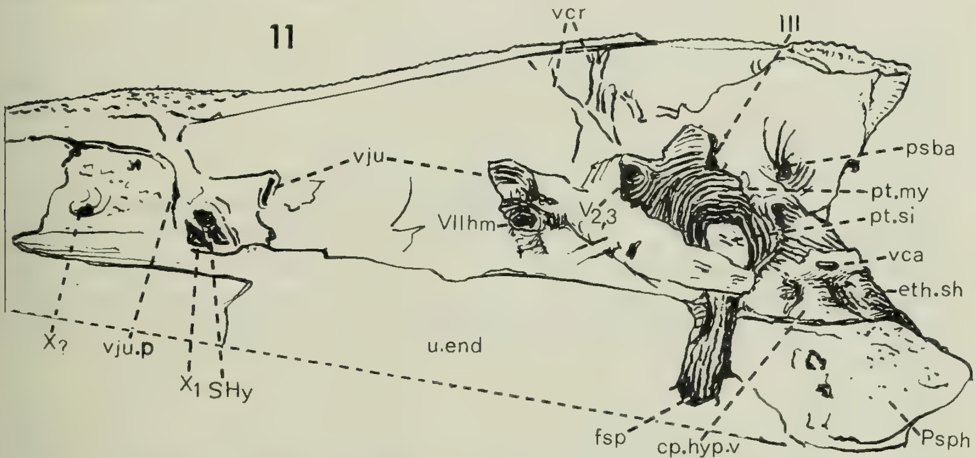

FIG. 11. *Parabuchanosteus murrumbidgeensis* (White). Right anterior half of fragmentary endocranium somewhat tilted upwards. P.48675 ×2. See Pl. 2, fig. 1.

That author has given a possible explanation of the 'extra-mural' position of the pituitary vein on embryological grounds, but it seems nevertheless remarkable to find this important difference in two genera, *Kujdanowiaspis* and *Parabuchanosteus* which have otherwise many features in common in this part. If the rectus externus muscles do come so far in, one may wonder why they would need such a powerful attachment.

Above the sinus on a level with the efferent pseudobranchial canal is a small foramen possibly for the oculomotor nerve (*III*) and further still to the rear at a somewhat lower level in the illustrations the broken exit of the 'trigeminus proper' ($V_{2,3}$), which corresponds reasonably well with Stensiö's interpretation of the details in *Kujdanowiaspis* (1963, text-fig. 17). Above $V_{2,3}$ are a number of small canals leading into the skull-roof possibly for nutritive vessels (*vcr*) (*cf.* Ørvig 1957 : 307, text-fig. 6) leading to the sub-cutaneous vascular plexus (see p. 393 *infra*). A little behind these near the floor of the endocranium is a section of the canal of the hyomandibular nerve (*VIIhm*) marking the position of the anterior postorbital process on this side, and attached to the canals upper surface as in dolichothoracids and coccosteomorphs (Stensiö 1963 : 282), is an anterior fragment of the jugular canal (*vju*) leading into the posterior myodomal space. A hinder fragment of this canal is to be seen similarly placed to the two canals (IX, X_1) extending from the posterior postorbital process, which is complete on the other (left) side (Text-fig. 4; Pl. 4, also Pl. 5, fig. 2).

The posterior postorbital process is an interesting development. When Stensiö (1945 : 12–13, 32, text-figs. 5–7) first dealt with this part in *Kujdanowiaspis*, in which it is forked, he described the posterior branch as being hollow and carrying the *v. posthyoidea lateralis* to the jugular vein. Later (1963 : 70, 82–84, text-figs 14, 41, 42*C*, 43, etc.) the two shanks are shewn to be solid and appressed to the underside of the paranuchal and postmarginal plates, and it was suggested that these shanks of the posterior process 'may very well have been formed from the posterior parts of two long, dorsal extra branchials originally belonging to the hyoid arch and to the branchial arch proper (the glossopharyngeus arch), respectively.'

The posterior postorbital process in *Parabuchanosteus* is very different and it is difficult to reconcile its form with the origin suggested above.

The jugular vein between the anterior and posterior postorbital processes runs entirely inside the endocranium in *Parabuchanosteus**, which it leaves by a large aperture at the base of the hinder face of the posterior process (*vju.p*). The latter is broad at the base and very long, and when undamaged reaches almost to the outer edge of the post-marginal plate. It lies directly under the post-marginal sensory canal and is therefore attached to the under-surface of the marginal for the greater part of its length and does not underlie the paranuchal plate at all, as it does in *Kujdanowiaspis*. It consists of a narrow tube for most of its length, as well preserved specimens show (P.33635, P. 33642), and then continues as a groove to the postero-lateral angle of the shield. At the proximal end immediately inside the endocranium it passes over the jugular vein just before the latter leaves the skull at *vju.p* (P.48675). This canal carries the first branchial trunk of the vagus nerve (X_1) and not the hyoid vein, as I first described it (White 1952; 272–4, text-figs 22–25). The process is completed by a well marked groove and ridge running along its anterior side for about one-third of its length. The groove continues a large canal which passes into that of the jugular vein; and which is now identified as that for the hyoid vein, although such a position, as Holmgren (1942 : 170) has remarked, is much further forward than is the case in sharks (*sh.y*, Text-figs, 4, 11; Pl. 2, fig. 1. *cf.* Westoll & Miles 1963 : 144, 150; Miles & Westoll 1968 : 403).

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* There seems to have been the same arrangement in *Stuertzaspis* (Westoll & Miles 1963 : 150, text-fig. 4), the supposed perforation of the anterior post-orbital process (*c.v.ju.m*) being the foramen of *VII hm*.

Nothing of any value has been found in the labyrinth area, but fragments are to be seen in P.48672 (*r.la.c.*, Pl. 1, fig. 1.) and in P. 33597.

The posterior postorbital process marks the anterior boundary of the large cucullaris depression (*dpmcu*), and inwards and backwards of the posterior opening of the jugular vein canal (*vju.p*) to the main exit of the vagus (*X*) the side of the endocranium is dorsoventrally concave for the attachment of muscle. Along this reach is a foramen (*X*?), perhaps for the second branchial trunk of the vagus, or for a vein. Behind the main vagus exit (*X*) the endocranium rapidly widens and shallows and ends in a more or less vertical wall, at least in the upper part, along the line of the posterior margin of the skull-roof between the articular processes. There is no discrete supravagal process but this is clearly represented by the postero-lateral corner or angle of the endocranium (*plae*, Text-fig. 2; Pl. 1, fig. 1; Pl. 4; Pl. 5, fig. 2; Pl. 7, fig. 3), and as will be seen later shows that the cranio-spinal process of Stensiö in coccosteids is a true supravagal process and nothing to do with the cranio-spinal process in petalichthyids.

The thickening of the skull-roof pierced by the canal for the endoskeletal division of the endolymphatical duct (*th.n*, *d.end.i*, Plate 4) is much as in *Kujdanowiaspis* (Stensiö 1963, text-fig. 42*C*).

Behind *X* and following the line of the narrowing endocranial wall are the apertures of the spino-occipital nerves (*spio*, Text-figs 2, 4; Pl. 5, fig. 2; Pl. 6, fig. 8). There appear to be at least 7. The anterior nerves appear to have only one large elongated aperture but the fourth and subsequent canals are double, having a smaller upper aperture for the dorsal branches. A few of these canals are very well seen in Pl. 5, fig. 2, coming from the cranial cavity, the only instance in this material when a substantial part of the cavity wall has been preserved, except part of the roof seen in P.48674 (*rcr*, Pl. 5, fig. 1), and the smooth median dorsal tract that runs the length of the underside of the fine skull, P. 48672 (*rcv*, Pl. 1, fig. 1). On either side of the tract in this as in other specimens (*e.g.* P.33592, P.33610, P.58443 etc., but especially P.33642) are vestiges of the subcutaneous vascular plexus already noted above (p. 392) and which have been described and figured in a specimen possibly of *Actinolepis* by Ørvig (1957 : 307, text-fig. 6).

The back of the skull (Text-fig. 2; Pl. 6, fig. 8) bears little resemblance to the types described by Stensiö (1969 : 223–246, *e.g.* text-figs 12, 21, 35, 124) of which the pholidosteid, that which is said to characterize the coccosteomorphs, is hypothetical.

In *Parabuchanosteus* the upper part of the back of the head is vertical and vested in perichondral bone. It is divided by a deep median groove into two very convex

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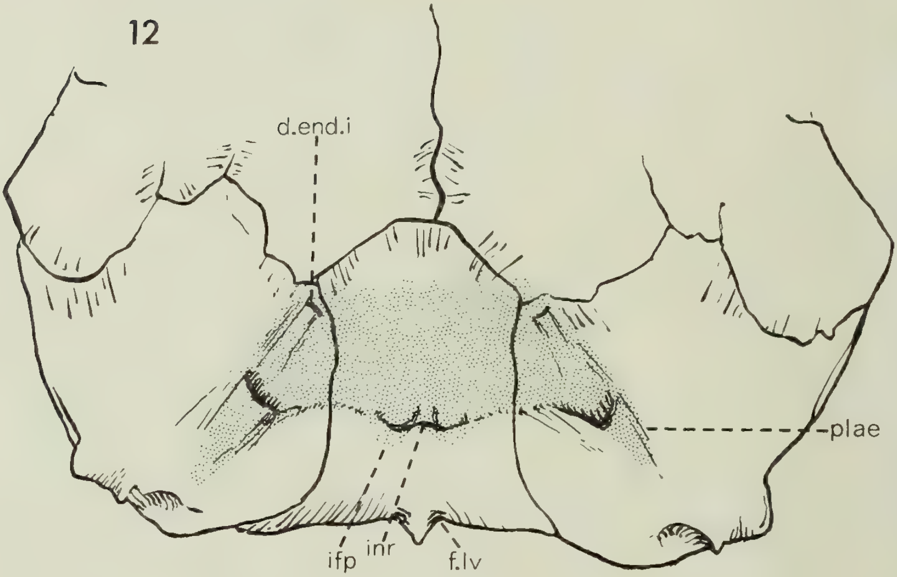
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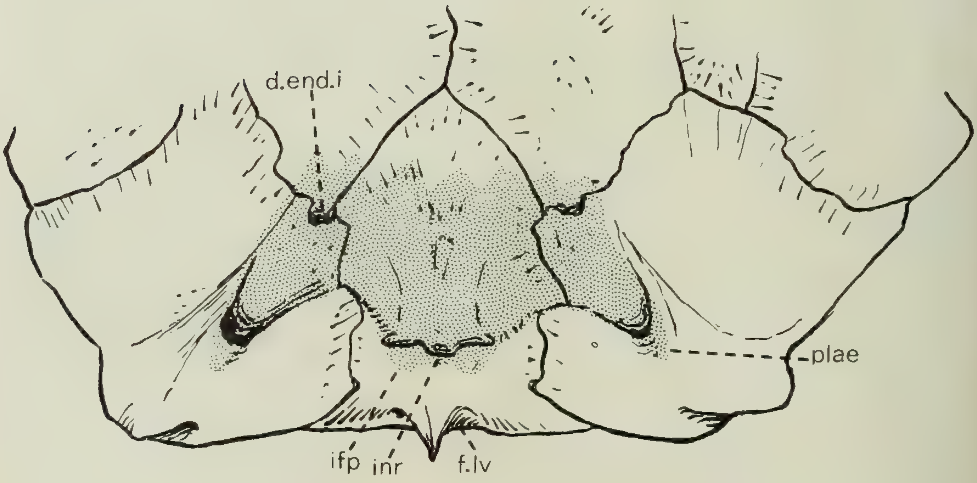
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FIGS 12, 13. Visceral surface of hinder part of skull-roof of two coccosteids from the Upper Devonian of Gogo, Western Australia to shew the form of the endocranial roof (stippled). P.50913, P.52551 ×2.

sides, the epiotic prominences (*Epio*), each with a deep pit (*fdv*) flanking the supraoccipital spine (*sos*), which fills the median groove at the top. A pair of well-marked foramina for post-cerebral veins (*pcv*) are at the bottom of the median occipital groove. The spine is attached to part of the skull-roof which appears to be a discrete dermal bone although fused indistinguishably, like the other larger dermal bones, into the skull-roof. In P.33597 (Pl. 5, fig. 2) the occipital surface is broken away and the supraoccipital spine is seen to have the form of an inverted cone. The pits on the occipital surface on each side of the spine have in them a small foramen for a vein (*vdm*), and are the proper areas of attachment for the levator muscles of the head (*f.lv*) and, as already suggested by Miles & Westoll (1969 : 400), not those so designated by Stensiö (1963, *f.lv*, text-figs. 54 *B-D* etc; 1969 text-figs 124, etc.), which are inside the endocranium and are so clearly seen in this specimen. These pits are here named the infranuchal pits (*ifp* Pl. 6, fig. 8*a*) and are separated by the median infra-nuchal ridge (*inr*). They were possibly filled with cartilage to strengthen the very thin endocranial back-wall.

The true arrangement is also shewn quite clearly by the Newcastle specimen of *Coccosteus* figured by Miles & Westoll (1968 pl. 1, fig. B) and Stensiö (1969, text-fig. 124D) and by two skulls of coccosteids from Gogo, Western Australia which Dr. Miles has kindly allowed me to examine and to figure (Text-figs 12, 13). In each case, especially clearly seen in the Australian specimens, the pits face forwards and, as Miles & Westoll have pointed out (1968 : 400, text-figs *2a*, 16*b*) could not have been for the levator muscles.

In these three specimens only the top of the posterior surface of the skull is preserved in bone (the posterior ascending lamina of Stensiö), and like the remainder of the endocranium, the rest was presumably cartilaginous; but what is present of the back of the skull slopes forwards over the infra-nuchal pits and not backwards as has been suggested in restorations of *Tapinosteus*, *Pholidosteus* and *Coccosteus* (Stensiö 1963, text-figs 46–49, 54 etc.). The true pits for the levator muscles are much smaller and fainter than in *Parabuchanosteus* but distinct nevertheless and in the same position on either side of the supraoccipital spine, which is much larger and completely fused with the back of the skull. There is no vertical median groove, nor are epiotic prominences developed.

The endolymphatic duct runs in a thickening within the endocranium as in *Parabuchanosteus* and *Kujdanowiaspis*, but the thickening is more centrally directed owing to the form of the endocranium.

It is not very difficult to derive this region of the endocranium from that of *Parabuchanosteus* or of *Kujdanowiaspis*.

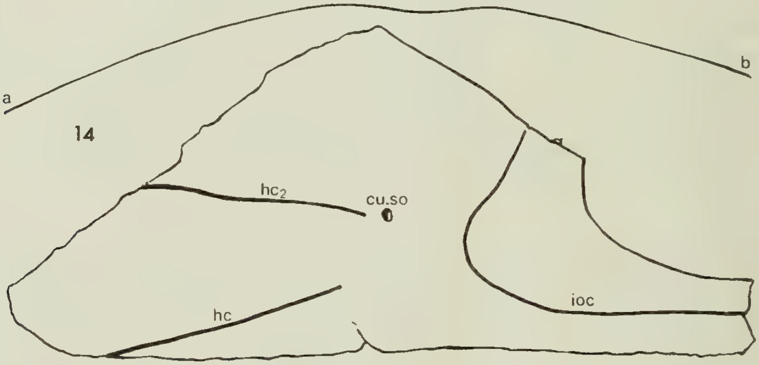
The cervical articular apparatus of *Parabuchanosteus* is very well developed (Text-figs. 2–4; Pl. 6, figs. 5, 7; Pl. 7), the fossa being broad and deep and the processes conspicuous on both the paranuchal and anterior dorso-lateral plates, although varying somewhat in detail. A curious feature of the joint is that in the only complete associated set (Pl. 7) when fitted together there is absolutely no possibility of movement between head and body-armour, even allowing for the articular lining.

ROSTRO-PINEAL BONE. A fairly complete example of the rostro-pineal bone (or rostral exoskeletal capsule of Stensiö 1963 : 115, text-figs. 10*A*, 42, 43) is present

(P.33612, Pl. 6, figs 1–4), and also the left side of this bone from a smaller animal (P. 33629). The former was identified by Dr. Roger Miles who has described it more fully in relation to other material (Miles 1971 : 185, text-figs 104, 105, '*Buchanosteus*'). It is complete on the right side but has lost its roof on the left, and the component bones, pineal, rostral, post-nasal and pre-rostral, if present, are completely fused together.

The triangular subnasal shelf or lamina (*sns*) fits closely on the ethmoid shield immediately below the anterior fenestra of the neuro-cranial cavity (*afcv*, Text-figs. 8–10), on each side of which is a well-marked groove for the optic nerve (*gr.II*).

The posterior face of the postnasal wall is hollowed out to form a deep transverse groove or cavity for the telencephalon (*c.tel*) with the cribrosal area on each side (*fno*, Pl. 6, figs 2, 4) for the passage of the olfactory nerve fila, and above there appears to be the much damaged pineal opening (*pi*). The olfactory tract must have been very short (*cf.* Stensiö 1963, text-fig. 38A). Laterally to the cribrosal



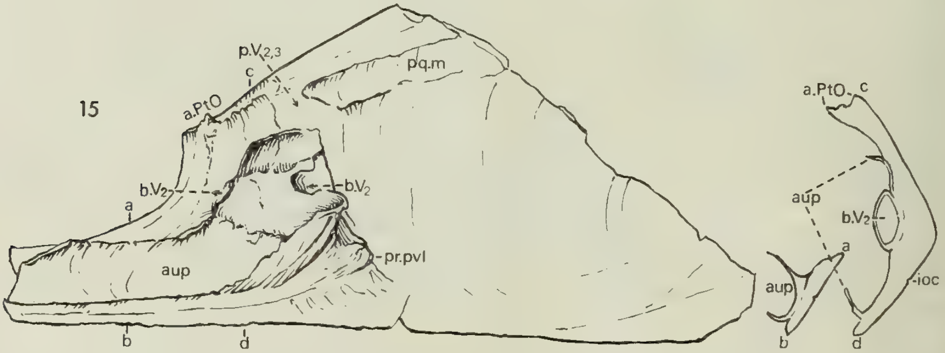


FIG. 14. *Parabuchanosteus murrumbidgeensis* (White).
Outline of right suborbital plate shewing sensory system *ab*, outer longitudinal curvature. P.50416 ×1½. See Pl. 8, fig. 3.

FIG. 15. Sketch of inner face of same specimen to shew seating of palatoquadrate. Vertical sections at *ab*, *cd*.

areas the groove of the postnasal wall opens out to form the orbito-ethmoidal 'slit' (*f.nv*) and above the main groove there is a smaller dorsal groove (*dg*) narrow in the centre but wider laterally, through which canals for the profundus (V_1) and the superficial ophthalmic (*oph.V*) nerves passed forwards through the wide internasal wall-space. This groove is continued at the side (*dls*) as far forward as the notch for the inhalent nostril and in it the lateral ophthalmic nerve passed through a short canal or arch (*oph. l*).

The internasal wall (*iw*) forms a large triangular cavity roughly coextensive with the sub-nasal shelf. In it are to be seen the remains of numerous canals for nerves and vessels.

The fenestra exonarhina communis is very large and the nasal cavity each side is divided into a smaller posterior division or depression (*pd.n.cav*) corresponding to the incurrent nostril and a much larger, wider, anterior division (*ad.n.cav*), for the exhalent nostril, and this in front was partly lined with dermal bone bearing denticles in front and medially (*dt*, Pl. 6, figs 1, 3).

There is no interfenestral process separating the nostrils externally and the inhalent nostril, the position of which is clearly indicated by a conspicuous denticulated groove, must have been immediately over the exhalent which was entirely cartilaginous. However, it is not difficult to see how the nasal region of *Kujdanowiaspis* (Stensiö: 1963: text-fig. 10*A*, etc.) could have been derived from such as that of *Parabuchanosteus* by the restriction of the fenestra and its subdivision by the development of the process.

Another bone belonging to the head region that may be referred to this fish with confidence is a right suborbital (Text-figs 14, 15; Pl. 8, fig. 3), which is complete except for the tip of the suborbital bar and the posterior margin. It fits reasonably well on to the middle-sized skull-roof (P. 48672, Pl. 1. fig. 1) although from a somewhat larger specimen, and shews how very forwardly directed the eyes must have been, the orbits being only 40° from direct forward vision. The plate is considerably curved longitudinally and dorso-ventrally. The latter curve is angular with the upper part twice as deep as the lower on the postorbital expansion. The pattern of the sensory system is remarkable. The infraorbital canal runs well behind the orbital continuing after the briefest of intervals the line on the postorbital. Behind it on the upward slope is a pit for a cutaneous sense-organ (*cu.so*) immediately followed by a sensory line gently inclined upwards and below this on the downward slope another line more steeply inclined downwards. This pattern of sensory organs so fully developed is rare in the group (*cf. Holonema:* Miles 1971 : 132, text-figs 32*A*, 33*A*). The lower line may be reasonably identified as the anterior part of the supramaxillary (supraoral) canal (*hc*, Stensiö 1947 : 53, text-figs, 12, 15*B*) while the upper line rather neatly occupies the 'primary position of the probably reduced middle division of the supra maxillary line' (hc_2), *ie.* the post-suborbital line of Miles and Westoll (1968 : 396).

The inner concave face of the suborbital plate is of great interest for the outer margin at least of much of the palatoquadrate was invested with perichondral bone and this is rigidly fused to the inner face of the suborbital plate (*aup, pq.m*, Text-fig. 15). The seating is broad and the outer margin of the autopalatine especially must have been massive. It follows the curve of the orbit and turns upwards giving off as it does a postero-ventral process (*pr.pvl—cf.* Stensiö 1963 : 232, text-figs 51*C*, 70, 77). Almost immediately above this the palatine is pierced by a very large foramen or arch ($b.V_2$), and shortly above this the seating of the autopalatine part is separated from that of the middle part of the palatoquadrate by a wide gap or broken arch ($p.V_{2,3}$). This gap is possibly for the passage of the maxillary and mandibular nerves, of which the former turned forwards and, joined by the lateral buccal nerve, passed through the lower arch ($b.V_2$). The seating of the middle part runs near and roughly parallel with the top of the plate and is only half the width of the autopalatine attachment, and in a fragment from a somewhat larger fish (P.33678) the whole surface is seen to have been covered in bone. The front of this margin at the orbit is broadened with large inner lateral denticles or pegs for attachment to the skull-roof (*a.Pto*, Text-fig. 15).

In general the arrangement of the palatoquadrate in this region bears a very fair resemblance to Stensiö's 'Tentative restoration' in *Kujdanowiaspis* (Stensiö 1963 : 123–5, 199, 206, text-figs 39*A*, *B*, 40).

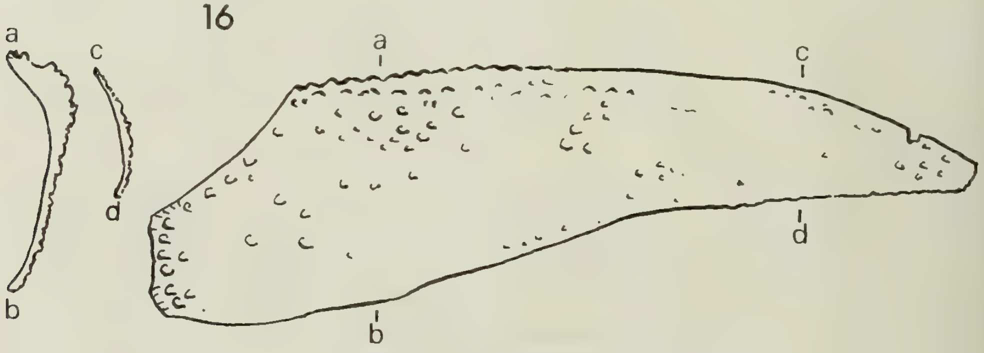


Fig. 16. *Parabuchanosteus murrumbidgeensis* (White).
Right sub-marginal plate with cross-sections at *ab*, *cd*. P.53260 ×3.

The only other part of the head identified in the collections, the submarginal plate, is represented by a single but complete specimen from the right side (Text-fig. 16). It is thin and internally concave, 370 mm long and 10 mm wide at the maximum. Both margins are gently curved, the lower concave except at the back, the upper convex, especially in front, and in spite of the universal tubercular ornament it shews a groove along the marginal contact. At the back it is cut away for the projection of the postmarginal plate.

Body-plates. The body-plates that may be considered in connection with *Parabuchanosteus* are few in number, not more than 13, thin like the head-shields but apparently even more fragile, for all are imperfect, mostly very imperfect, with few margins to establish their shape directly, and generally from smaller animals than the heads.

There is, of course, the difficulty inherent in all assemblages of isolated plates where more than one species is represented (which is here clearly shewn by the presence of two very different types of posterior ventro-lateral plate) of sorting them correctly, particularly in this instance where the ornament is similar in several species.

Fortunately the only associated plates, the imperfect and rather small but finely preserved paranuchal and anterior dorso-lateral plates (Pl.7), provide with their overlapped areas a clear link between the heads and the isolated plates of the back and sides.

There are six examples of the median dorsal plate (*MD*), P.33583, P.33672, P.50346–7, P.50357, P.50389, which although each is imperfect, together give a fair idea of its form (Text-fig. 7; Pl. 8, figs 1, 2).

The shape is simple, perhaps deceptively so, with a straight anterior margin, almost straight sides (there is a slight waist) and an obtuse posterior spine—features that can be found, at least separately, among either coccosteomorphs or pachyosteomorphs (Gross 1932). The plate is fairly elongated, with the maximum breadth over the curve a little less than one-third of the median length, the most complete specimen measuring approximately 48 mm × 155 mm. The transverse curve in front carries on the angular curve of the back of the head, but it flattens out towards the rear, since the plate, which is almost straight in profile for rather than half its length, droops to the posterior angle.

The surface is covered with small, evenly spaced stellate tubercles similar to those on the other plates (Pl. 8, fig. 5), and there is no sign of the main lateral line, so conspicuous in coccosteomorphs but absent in pachyosteomorphs.

The chief feature of the concave visceral surface is the long median keel with its large intermuscular or carinal process at the rear (*ke*, Text-fig. 17). The keel varies in its forward extension, approaching closely to the anterior margin of the plate in one specimen (Pl. 8, fig. 2) but falling far short in a somewhat larger specimen (P. 50347). It keeps low with a sharp edge until it rises rapidly to form the process at about the middle of the length of the plate, and at the same time the edge splits to form the groove for grasping the neural spines of the vertebral column and continuing upwards behind to form an oval depression to grip the submediandorsal plate (Miles & Westoll 1968 : 423). The process is at the growth-centre of the plate some distance from the tip of the posterior spine, and there are the usual butresses, faint at the sides, far more marked behind where the process is produced backward, especially in the largest specimens (P.50357). There are no 'anteriorly facing pits', as mentioned by Miles & Westoll.

The areas overlapping the dorso-lateral plates are very well shewn. That for the anterior plate is unusually short and broad, that for the posterior plate exceptionally straight and narrow. The anterior area corresponds exactly with the smooth overlapped area on the anterior dorsolateral plate figured in Plate 7, and thereby fixes the limit of its missing hinder margin. The long narrow overlapping area of the median dorsal plate and the posterior margin of the anterior dorso-lateral plate mark the upper and anterior margins of the exposed surface of the missing posterior dorso-lateral plate, while the hinder ventral overlapped area of the anterior dorso-lateral establishes the front margin of the unknown posterior lateral plate.

The anterior dorso-lateral plate is represented by a single example, fortunately the fine almost complete specimen associated with the paranuchal previously mentioned

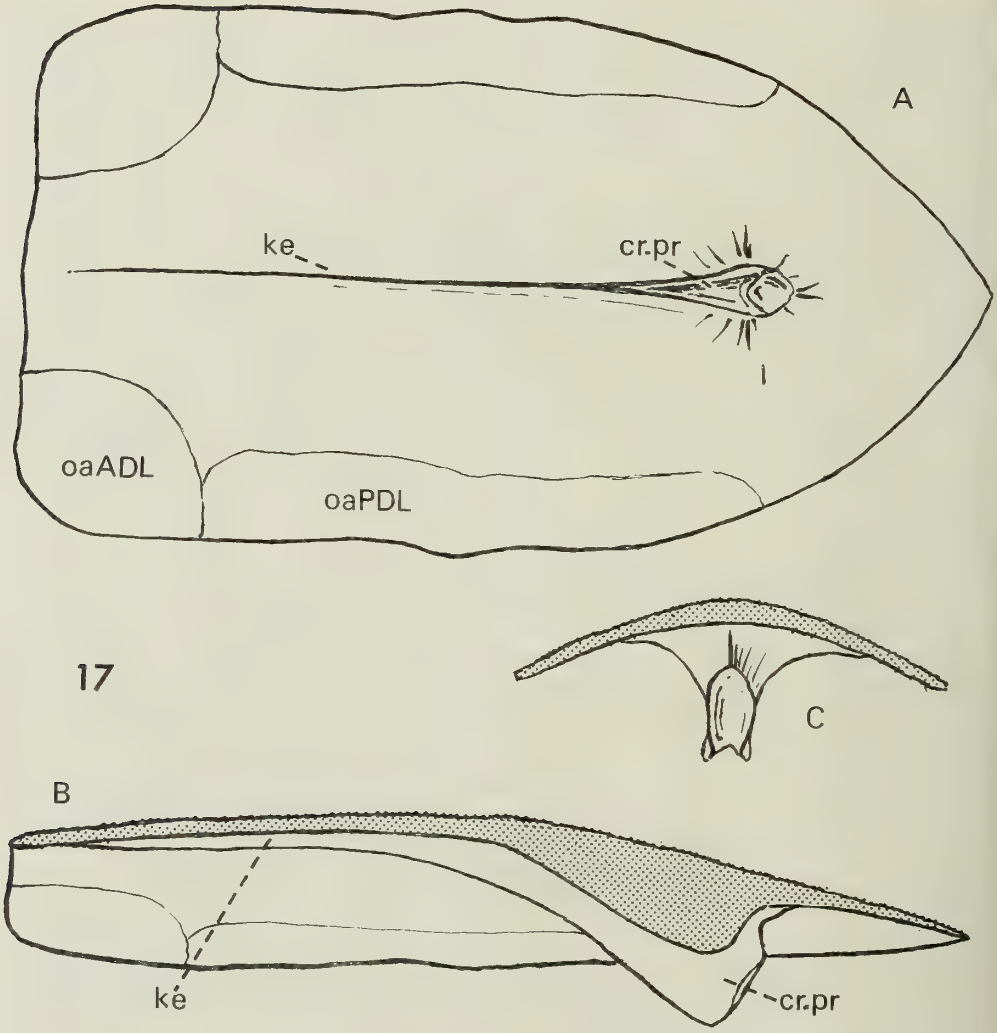


FIG. 17. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of median dorsal plate. A, ventral view. B, left parasagittal view.
C, posterior view of intermuscular crest. All × 1½. See Pl. 8, fig. 2.

(Pl. 7, figs 2, 4). Judging by the overlapping areas on the median dorsals there is only an oblique strip missing along the hinder border. The articular apparatus is very fully developed, both glenoid condyle and sub-glenoid process being very prominent, and as remarked above, they fit very closely into the process and fossa of the associated paranuchal plate.

The exposed area is relatively small, the plate being very short and the overlaps large, that for the median dorsal being almost square with a selvage for the extrascapular. The area overlapped by the anterior lateral is short, pointed, very wide and deeply grooved parallel with the front margin, and behind it, separated by an acute projection of the exposed surface and a ridge, is an overlapped area for the posterior lateral plate, which is, so far as we know, unique. The exposed surface of the plate is finely tuberculated, as on the other plates, and bears deeply incised grooves for the sensory lines, the plan of which fits in reasonably well with that put forward by Ørvig (1969*a*), their disposition (P.l 7, fig. 2) being similar to that on the same plate in *Holonema* (Miles 1971: 158, 191, text-figs. 68, 70). According to their interpretation the main lateral line, after a brief entry in a deep groove from the paranuchal plate gives off a short mesially directed 'accessory twig' (*lac*) and then

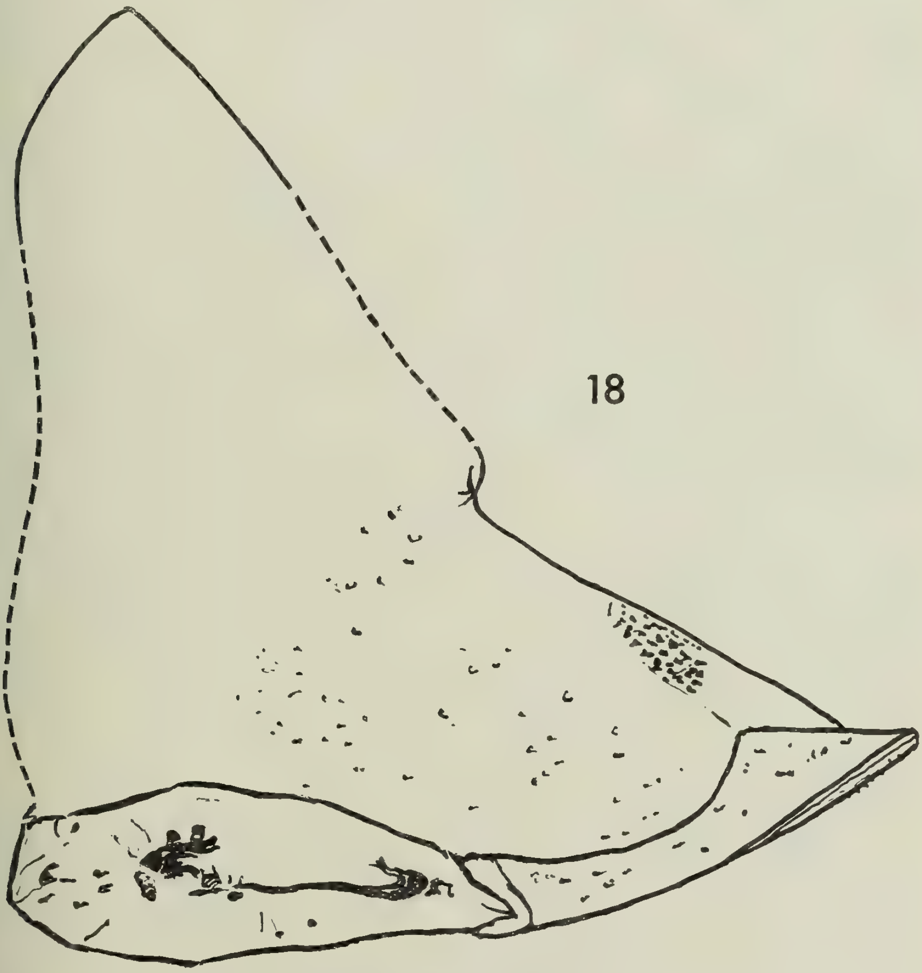


FIG. 18. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of right anterior lateral plate based partly on overlapped area in anterior dorsolateral plate and partly on specimen P.50248 (Pl. 8, fig. 4), with socket of pectoral fin, and spinal plate. ×2 approx.

is interrupted, running after a short break in a narrower groove (*mlc*) more or less directly backwards, possibly on to the posterior dorsolateral plate (Text-fig. 24), while the deeper groove thereafter continues parallel, apart from a kink, to the sloping anterior lateral margin, presumably on to the posterior lateral plate and supposedly holding the ventrolateral sensory line (*lcvl*).

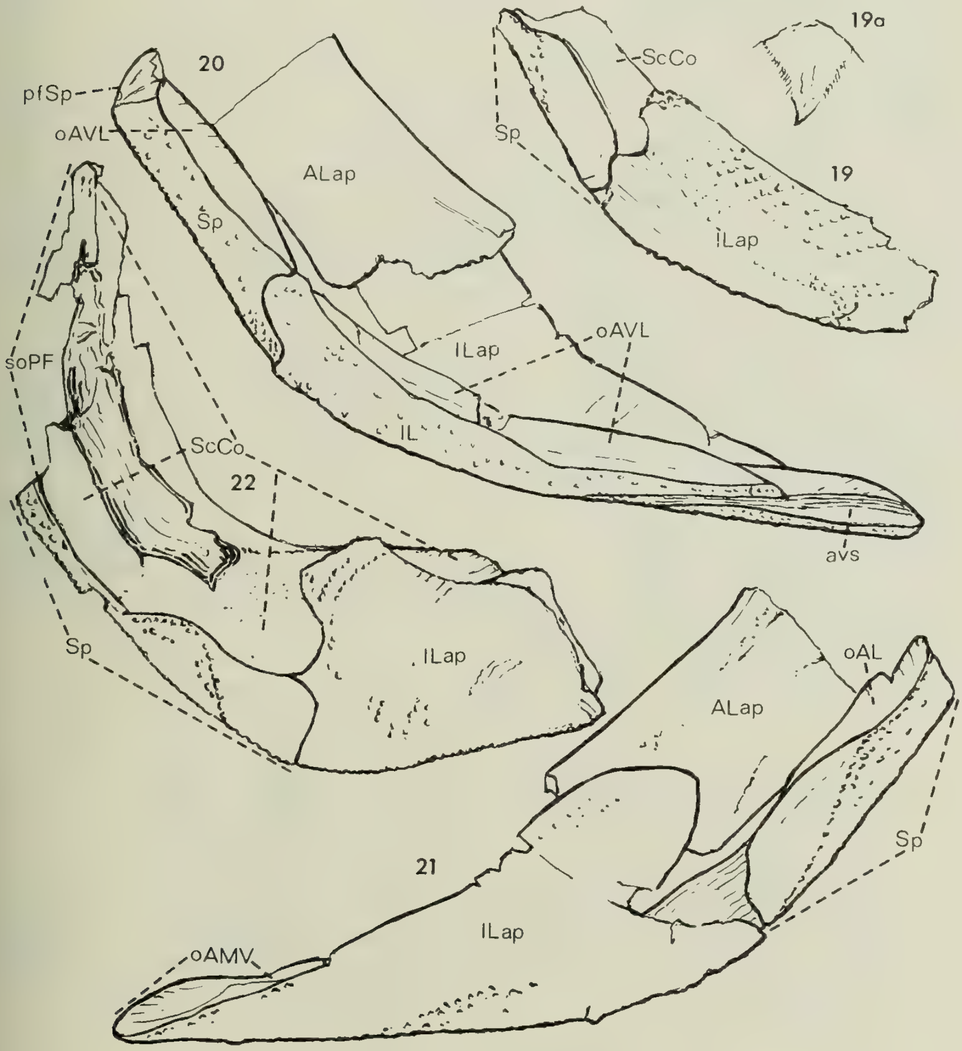
There is no indication of an anterior dorsolateral sensory line.

Of the missing posterior dorso-lateral plate we know only the length and curve of the upper margin from the underlaps on the median dorsal, but presumably it does not differ very much from the coccostean pattern (Miles & Westoll 1968, text-fig. 43).

With regard to the lateral plates there is equal difficulty. From the shape of the overlap on the anterior dorsal lateral plate, the upper end of the anterior plate was unusual, narrow and pointed, and the rather small specimen of the lower half assigned to this species is imperfect (Text-fig. 18; Pl. 8, fig. 4). The apron fits accurately on to that of the interlateral plate by which it is overlapped and the lower margin fits well on to the overlapped margins of the spinal plates. How far over the articular area of the scapulo-coracoid it extends it is not possible to be sure, but since the shoulder-girdle is distinctly coccosteomorph in character it is probable that it reached right over it to meet the posterior ventro-lateral plate. This basal part of the anterior lateral is very convex and sweeps round to the very broad upper part of the apron in an almost continuous curve for 90°. This part of the apron is, however, flattened and is roundly indented below by the overlap of the interlateral part and finishes at the upper end in a rounded point at the level where the side of the plate thickens and projects forwards, forming in this broken specimen a thick boss. The ornament on the sides is of the usual tubercular type, but this passes rapidly where it turns to form the apron into the special ornament of that part, which is best seen on a fragment of the interlateral plate (Text-fig. 19; Pl. 9, fig. 3). This ornament is similar to that in *Williamsapsis* (White 1952 : 265, pl. 28, fig. 1) but differs in detail and is somewhat variable: the teeth are less flattened, more finely striated and pointed and more strongly denticulated laterally: the ornament may be described as being composed of small depressed, biconvex, triangular teeth arranged in alternating rows and directed outwards with the upper surfaces finely striated with sharp downwardly curved points and finely but clearly denticulated along the sides except at the tips (Text-fig. 19; Pl. 9, figs 2–4). At the top outer part of the apron is a smooth area which is continued on to the spinal plate, a development apparently peculiar to this species.

Much of the apron with its special ornamentation is carried by the very long interlateral plate (Text-figs 19–22; Pl. 9) which, as suggested by Denison (1958 : 532), is true of *Williamsaspis*; the apron is very large and reaches from its spade-shaped overlap of the anterior lateral plate to the very tip in the centre. The interlateral (or clavicle) is very like that of *Coccosteus* (Miles & Westoll 1968 : 437, text-fig. 42) with anterior ventral sulcus (*avs*), groove for the coracoid process, and overlaps, but it is much longer with the details somewhat exaggerated, while the angle between the ascending and ventral laminae is much more acute. The ventral lamina is flat with the usual tubercular ornament and directed far more definitely upwards (Text-fig. 23).

The spinal plate (*Sp*, Text-figs 18–23; Pl. 9) is long and straight with no suggestion of a spine. The small triangular posterior face is almost flat with a shallow double groove to which perhaps the base of the fin membrane was attached. The slightly concave upper surface and the flat uptilted lower surface meet, like those of the interlateral, at a very acute angle, Stensiö's 'horizontal crest' (1959 : 8). The surfaces are uniformly ornamented with tubercles except that, as mentioned above, the upper anterior surface has a smooth triangular area in continuation of the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21
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ILap
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FIGS 19–22. *Parabuchanosteus murrumbidgeensis* (White).
Sketches of specimens shewn in Pl. 9 with lettering. 19*a*, denticle of apron much enlarged.

apron of the interlateral plate. The interlateral overlaps the spinal both above and below, and there are also considerable areas overlapped by the anterolateral plate along the upper margin and by the anterior ventrolateral plate along the lower.

An interesting feature of the shoulder-girdle is the superficial ossification of the massive scapulo-coracoid (Text-figs. 18, 19, 22–24; Pl. 9, fig. 4), which is surprisingly strong. As Stensiö (1958 : 9) and Miles and Westoll (1968 : 443) have noted, an ossified coracoid process has not been found in the known coccosteomorphs, only in certain dolichothoracids, but presumably this is an effect of the general reduction in ossification and therefore an index of age and not of relationship. In section it is roughly triangular where it is broadest at the bend at the interlateral-spinal junction.

It is very broad indeed at this point and also deep (Text-figs. 22, 23), but narrows quickly towards the midline. Apparently it does not meet its antimere, for the groove in the interlateral stops some distance from the mesial tip where the latter turns upwards to overlap the anterior median ventral plate (*oAMV*, Text-fig. 21). Posterior to the spinal plate the scapulo-coracoid narrows gradually, becoming wedge-shaped behind the attachment area of the pectoral fin (*soPF*), which is very long, as long as the spinal plate, and here much of the articular surface remains, but the details of foramina are not well preserved.

Judging from actual specimens this part most nearly resembles, not unexpectedly, that of the spineless *Williamsaspis*, rather than that of *Pholidosteus* with its prominent pectoral spine (Stensiö 1959, text-figs. 9–11, 58), but it comes near enough to Stensiö's prediction for *Plourdosteus* (1959, text-fig. 12). Clearly this massive support must have borne a very large fin.

A fracture in the pre-coracoid part shews the inner surface with canals for dorsal cutaneous nerves and vessels.

A noteworthy character of this scapulo-coracoid is the smooth inner curve without any indication of scapular process (anterior mesial angle) or of post-pericardial angle. Presumably such simplicity is primitive.

Of the ventral plates of the body there is none that can be definitely associated with this animal that has sufficient margins to be worth description.

III. SUMMARY OF CHARACTERS

The outstanding features of *Parabuchanosteus murrumbidgeensis* are:—

1. Separate rostro-pineal bone and short wide preorbital plates with complete mesial contact.
2. Orbits large and directed obliquely forwards.
3. Sensory canal system and pattern of dermal head-bones as in brachythoracids with large broad-based nuchal more than one-half median length of shield.
4. Cervical articulation very well developed but skull apparently immovable on body armour.
5. Neurocranium wide and flat, fused to skull, not unlike that of *Kujdanowiaspis*.
6. Parasphenoid roughly triangular with strong but incomplete transverse groove and very small paired bucco-hypophysial openings.

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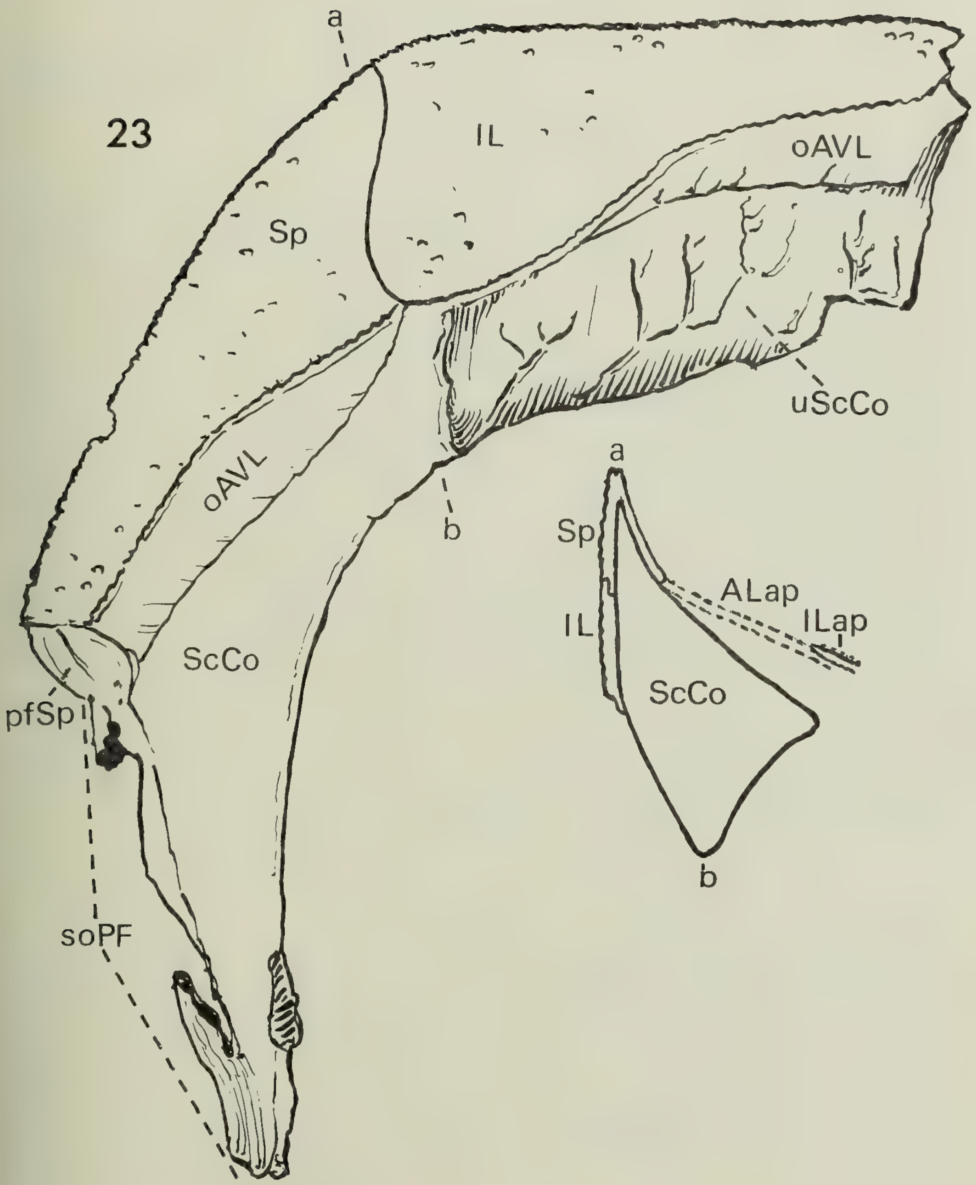
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a
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IL
ScCo
b

FIG. 23. *Parabuchanosteus murrumbidgeensis* (White).
Sketch of underside of interlateral and spinal plates with scapulo-coracoid. Cross-section at *a-b*. Same specimen as in Text-fig. 22, ×2½.

7. Inferior division of fossa hypophyseos in stout capsular dorsal extension of parasphenoid.
8. Wide sub-pituitary fenestra below large pituitary sinus.
9. Neurocranial cavity with large anterior fenestra.
10. Posterior postorbital process tubular, carrying 1st branchial trunk of vagus.
11. Posterior face of endocranium with paired epiotic prominences separated by small supraoccipital spine.
12. Suborbital plate with strong suborbital bar and wide dorsal groove for articulation with skull-roof.
13. Infraorbital sensory canal prominent on suborbital plate, but supraoral canal does not meet it. Cheek-line (postsuborbital line) and pit for cutaneous sensory organ present.
14. Palatoquadrate strongly attached to inner face of suborbital plate.
15. Submarginal plate resembling that in *Coccosteus*.
16. Median dorsal plate long and narrow with blunt posterior angle, well developed median keel and carinal process.
17. Small anterior dorsolateral plate overlapped by posterolateral as well as by anterolateral and median dorsal plates.
18. Posterior dorsolateral plate with long upper margin overlapped by median dorsal plate.
19. Anterolateral plate with narrow pointed top and wider base and apron.
20. Spinal plate without spine, upper and lower surface almost flat meeting at very acute angle, and posterior face very small, triangular. Smooth area on front upper surface continued from interlateral, forming part of apron.
21. Interlateral long and tapering with wide apron behind, and upper and lower surfaces meeting at acute angle.
22. Scapulo-coracoid massive with relatively strong investment of perichondral bone; section curved triangular in coracoid region.
23. Base of pectoral fin long and fenestra equal to spinal plate in length.

The essentially dolichothoracid characters are in (1) and come reasonably close to Denison's diagram of *Kujdanowiaspis* (1958, fig. 105*F*).

The neurocranium (5) at first sight, like the palatoquadrate attachment (14) seem clearly dolichothoracid features and bear no resemblance to the corresponding parts in the two coccosteomorphs, *Pholidosteus* and *Tapinosteus*, in which they have been described. But as Stensiö (1959 : 55) has sagely observed, the differences may be 'due to the fact that *Pholidosteus* and *Tapinosteus* both are upper Devonian forms whose endocrania have, perhaps, undergone considerable modifications and reductions and therefore differ from the endocranium in the geologically older Coccosteomorphi, for example *Coccosteus*. Since, however, the endocranium is practically unknown in the latter Coccosteomorphs, the question concerning the mutual kinship between the Coccosteomorphi and Dolichothoraci must be left unanswered for the present.' It is possible that the answer does lie in *Parabuchanosteus* and that some at least of features 6–11 belong to the original common design.

Paragraphs 12, 15, 16, the general form of the known body-plates and the large orbit are undoubtedly coccosteomorph in pattern, but shew peculiarities of their own, and this applies to the spineless spinal plate, which although it does occur in the aberrant contemporary *Williamsaspis* is not, as we know them, typical of the dolichothoracids.

IV. RELATIONSHIPS

The information about *Parabuchanosteus* introduces some new factors in the vexed dispute about the relationships of two major groups of arthrodires, the brachythoracids and the dolichothoracids (arctolepids) which is briefly summarized by Denison (1958 : 536, 547), 'if one follows Stensiö in considering a wide-based pectoral fin to be primitive among arthrodires the Arctolepida could not have been ancestral to the brachythoraci'. The idea that the arctolepids were ancestral to the brachythoracids is the holy writ of virtually all other workers on the arthrodires, and their views at times have been expressed, we think, with rather more vehemence than the evidence warrants. To quote Denison further 'But with the exception of this purely theoretical consideration, there seems to be every reason for believing that the Brachythoraci were derived from the Arctolepida. In the first place, Arctolepida lived at the right time. Secondly, there are several forms known that are intermediate in structure . . .'. Which considerations are purely theoretical in this discussion and which are not is largely a matter of subjective interpretation and Stensiö's contention is no more theoretical than are many of his opponents' notions: it certainly has more reasons for acceptance than the sweeping statement that 'there seems to be every reason for believing that Brachythoraci were derived from the Arctolepida' which, taken literally, is just not true; and ten such trivial and largely quantitative characters as 'the supraorbital lines may extend . . .', 'the trunk shield is rather high . . .' and so on, are hardly worth serious consideration in this context. Furthermore, isolated adult forms, however well they may show intermediate characters, need prove nothing more than some degree of common ancestry without the evidence that one group was fully developed before the other: otherwise the evidence is equivocal and may be read either way (*cf.* Van Valen 1963 : 261).

The time of the first appearances of the two groups is the crux of the argument and Denison put as first of his 'every reasons' for the derivation of the bracyhthoracids from the arctolepids that 'Arctolepida lived at the right time'. But living at the right time is not quite the same as first appearance and it does seem that people have been influenced by maximum developments, which, however impressive, are totally irrelevant to the argument; but they are easily demonstrated and generally based on reliable evidence accumulated over the years, whereas first appearances are liable to be moved backwards by fresh discoveries and one more authenticated specimen can destroy the current argument.

Until the 'intermediate' forms, all from the Siegenian, had been properly evaluated the prior claim of the arctolepids seemed clear enough: according to Westoll (1967 : 84) the earliest arctolepids recorded appear to be indeterminable remains from the Clee district, while the heyday of the group was in the late Lower Devonian (Denison

1958 : 502–3); whereas the typical brachythoracids started with *Coccosteus* in the late Middle Devonian and (with the 'pachyosteomorphs') had their maximum development in the early Upper Devonian (Miles 1969 : 133). The supposedly wide gap between the first record of an arctolepid (?Upper Gedinnian) and the début of the brachythoracids (Givetian) seemed to provide logical, almost incontrovertible, evidence for the ancestral position of the former group, hence the 'cri du coeur' from Westoll (1958 : 203) that Stensiö had turned the geological succession upside down! The position has been considerably changed within recent years: the three so-called 'mixed' genera from the Northern Hemisphere, *Euleptaspis* (*Leptaspis* Gross, 1933 : 62; Ørvig 1960 : 305 footnote), the giant *Tityosteus* (Gross 1962) and *Gemuendenaspis* (Miles 1962), have all been accepted as true brachythoracids and all are from the Siegenian (Miles 1969 : 153).

On the other hand, of the five indeterminable fragments from the Welsh Borders, noted by Westoll (1967 : 84) as being of lowest Dittonian age and therefore probably representing the first dolichothoracid record, all but one rather insignificant and doubtful spine are actually higher in the succession than the specimens of *Heightingtonaspis* [*Kujdanowiaspis*] *anglica* (White 1961 : 26; 1969 : 305), of which the lowest comes from beds 600 feet above the 'Psammosteus' limestone and may be of early Siegenian age. So the difference between the earliest records of the two groups has been so reduced as to call into question the validity of the stratigraphical evidence in the argument.

Miles (1969 : 128, 147, 165) in his paper on placoderm diversification suggests that this took place rapidly after the appearances *inter alia* of heavy armour forming a separate head- and trunk-shield and a cervical joint, not long before they appear in the geological record, when the major taxa become distinct. The brachythoracids were derived, he suggests, from dolichothoracids, from unknown unspecialized ancestors at the base of the phlyctaenaspid stock, presumably without the specialization of the exaggerated pectoral spines of the familiar forms and possibly also of the considerable length of the body-armour. This would be in accord with the 'generally accepted view' which De Beer (1951 : 98) quotes 'that it is not possible to derive one form in phylogeny from another if the latter is too specialized'. Whether the length of the body-armour is a specialization is open to question. One of us has suggested (White 1952 : 296) that long body-armour of the dolichothoracids together with the long-based fin of the brachythoracids were characters of the common ancestor of the two groups, and this combination has persisted in the Siegenian brachythoracid *Gemuendenaspis* (Miles 1962) in spite of Denison's (1958 : 539) difficulty in imagining 'how this could be'. We still lean towards the common ancestor as being the true explanation of the origin of these groups and would suggest modifying Miles' idea so as to place the derivation of the brachythoracids at the base of the *actinolepid* stock.

At this point the pre-actinolepid might be indistinguishable from a common ancestor.

The case of *Parabuchanosteus* is very different from that of the Siegenian genera of the Northern Hemisphere mentioned above. Although its brachythoracid features are perhaps the more obvious, its dolichothoracid qualities are clear enough. It has,

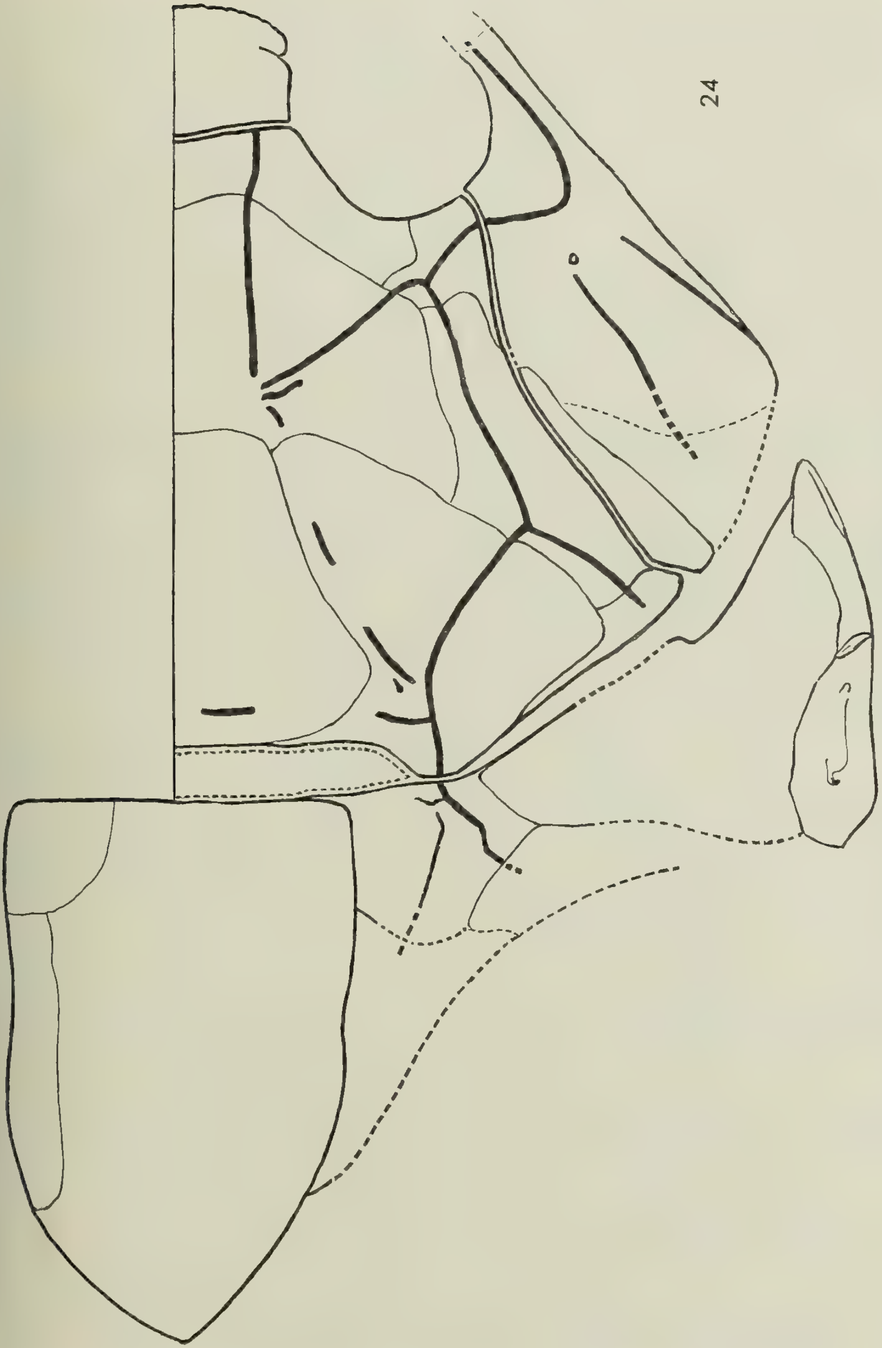

Fig. 24. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of right side of head- and body-armour (median dorsal plate complete to shew overlaps).

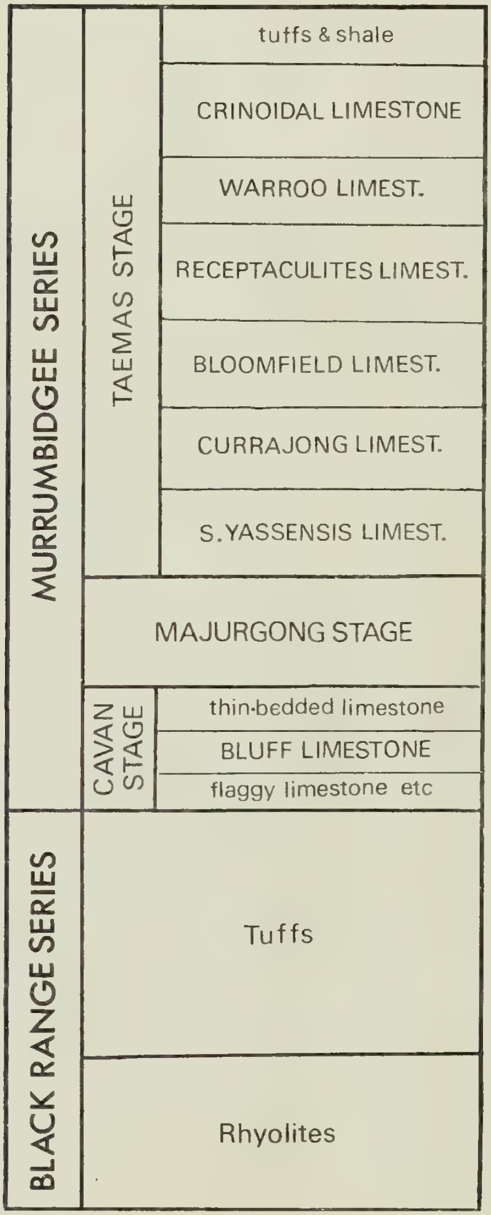
MURRUMBIDGEE SERIES
TAEMAS STAGE
tuffs & shale
CRINOIDAL LIMESTONE
WARROO LIMEST.
RECEPTACULITES LIMEST.
BLOOMFIELD LIMEST.
CURRAJONG LIMEST.
S. YASSENSIS LIMEST.
MAJURGONG STAGE
CAVAN STAGE
thin-bedded limestone
BLUFF LIMESTONE
flaggy limestone etc
BLACK RANGE SERIES
Tuffs
Rhyolites

FIG. 25. The stratal subdivisions of the Taemas area. From Pedder, Jackson and Philip, 1970, after I. A. Browne, 1959.

of course, been acclaimed as a true intermediate between a dolichothoracid ancestor and a brachythoracid descendant, or, to put it another way, as a brachythoracid throwing off the last effects of a dolichothoracid past. But the distribution of the characters is odd—there is not so much of a mosaic effect about them as that of a linear series: dolichothoracid at the snout, normal brachythoracid over most of the skull-roof, and specialized brachythoracid (with perhaps even a touch of pachyosteomorph) body-armour. To claim that one part was more ancestral in type than the rest would conjure up a curious picture of a creature that was part of a phylogenetic assembly-line gradually moving up the scale, with a reactionary snout soon to be discarded and a progressive backside leading the way to better things. On the contrary we see *Parabuchanosteus* as a prime example of experimentation (Schaeffer 1965; 1967 : 1–6) in which coming events have cast a longer shadow than usual.

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The specimens were prepared in acid by Messrs. R. Croucher, P. Whybrow and C. I. Macadie, and the photographs for the plates were taken by Mr. Peter Green, of the Museum Photographic Service.

VI. LOCALITIES

Localities, as written on labels, from which identifiable remains of *Parabuchanosteus* were collected by H. A. Toombs.

A. April to May 1955

1955.

2. *S. yassensis* Limestone
Not *in situ*, left bank of Murrumbidgee, on shore at bottom of scree slope below 'Shearsby's Wallpaper', 1100 yds upstream from Old Taemas Bridge. (=63/3). P.33202, P.33582, P.33583.

4. *S. yassensis* Limestone (near base)
Sloping ground immediately north of 'Shearsby's Wallpaper', 1700 yds at 154° magnetic from Taemas homestead. P.33592.

6. *S. yassensis* Limestone (near base)
Loose blocks near 55/5, not *in situ*, but probably nearly so. (=63/16). P.33597.

12. *S. yassensis* Limestone
Left bank of Murrumbidgee, 80 paces downstream from mouth of Oakey Creek, low cliff c. 1300 yds upstream from Old Taemas Bridge. P.33610.

14. *S. yassensis* Limestone
Spur above left bank of Murrumbidgee, 2250 yds bearing 55° magnetic to centre of New Taemas Bridge. P.33612.
15. *S. yassensis* Limestone
Loose blocks on hillside around 55/14 (*c. in situ*). P.33613, P.33618.
19. Bloomfield Limestone (near base)
Gully in left bank of Murrumbidgee, 3650 yds at 344° magnetic from Majurgong T.S. P.33629.
23. *S. yassensis* Limestone
Loose blocks *c. in situ*, on west limb of anticline and south slope of valley, 850 yds at 71° magnetic from Majurgong T.S. P.33635.
26. *S. yassensis* Limestone (near base)
On north side of hill, 1150 yds at 67° magnetic from Majurgong T.S. P.33642, P.51644.
32 & 33.
Near Bloomfield-*Receptaculites* boundary
On west side of main road, *c.* 100 yds N. of junction with road to Cavan: scattered blocks along strike line 50 to 100 yds from road, 1400 yds SSE of centre of new Taemas Bridge. P.33672, P.33673, P.33678, P.33683, P.53260.
x. ?Cavan Bluff Limestone
N. side of Bloomfield Rd, 1⅝ miles NE of Old Taemas Bridge, and 10 miles SSW of Yass. P.33430 (Colld. D. J. Cameron).

B. March-July 1963

1963
3. *S. yassensis* Limestone
Left bank of Murrumbidgee, 1100 yds upstream from Old Taemas Bridge, at bottom of scree slope below 'Shearsby's Wallpaper' (=55/2). P.48672, P.48674, P.50345, P.50346, P.50347.
7. *S. yassensis* Limestone (near base)
Right bank of Murrumbidgee, on shore, *c.* ½ mile downstream from Fifeshire Creek. P. 50357.
11. *S. yassensis* Limestone
Right bank of Murrumbidgee, *c.* ½ mile downstream from Fifeshire Creek, on NE point of small inlet. P. 50364.
12. Warroo Limestone (near base)
Right bank of Murrumbidgee at N end of cliffs, on shore, 2200 yds at 15° magnetic from Majurgong T.S. P.50367.
13. *S. yassensis* Limestone
Right bank of Murrumbidgee on shore, S. side of creek 1½ miles W of S of Alum Creek road-bridge. P.50378.
14. *S. yassensis* Limestone
Right bank of Murrumbidgee on shore, N side of creek 1½ miles W of S of Alum Creek road-bridge. P.50382.

16. *S. yassensis* Limestone (near base)
Left bank of Murrumbidgee on shore east of mouth of Oakey Creek, 1250 yds upstream from Old Taemas Bridge. P. 50389.
24. *S. yassensis* Limestone (near top)
Shore at south end of "Goodradigbee Lake", immediately east of where track from Barber's and Wee Jasper ends. P.50408.
25. *S. yassensis* Limestone (platy limestone near middle)
Shore at south end of "Goodradigbee Lake', east of 63/24. P.50416.
41. *S. yassensis* Limestone
Right bank of Murrumbidgee at most westerly point, 1850 yds at 24° magnetic from Majurgong T.S. P.50443.
58. Warroo or *Receptaculites* Limestone (near junction)
Right bank of Murrumbidgee, 3150 yds at 70° magnetic from Majurgong T.S. P.50808.
60. *S. yassensis* Limestone (low)
Right bank of Murrumbidgee, boulders probably nearly *in situ,* on shore and up hillside, 2500 yds due E of Majurgong T.S. P.50219.
66. *S. yassensis* Limestone
Left bank of Murrumbidgee, boulders on shore and hillside above, 1300 yds at 29° magnetic from Majurgong T.S. P.48675, P.48676, P.50248, P.50249.
68. *S. yassensis* Limestone
On hillside 1100 yds at 35° magnetic from Majurgong T.S. P.50252.
70. *S. yassensis* Limestone
Left bank of Murrumbidgee, on shore, probably *c. in situ,* 1400 yds at 62 magnetic from Majurgong T.S. P.50262.
83. *S. yassensis* Limestone
Top of spur falling west to left bank of Murrumbidgee, 1800 yds at 347° magnetic from Majurgong T.S. P.50323.
88. Crinoidal (? or Warroo) Limestone
Left bank of Murrumbidgee, scattered blocks on hillside 3650 yds at 9° magnetic from Majurgong T.S. P.50335.

DISTRIBUTION OF SPECIMENS

Specimen		Locality	Specimen		Locality
P.33202	—	55/2 (g)	P.33635	—	55/23
P.33430	—	55/X (a) (h)	P.33642	—	55/26
P.33582	—	55/2	P.33672	—	55/32 (c)
P.33583	—	55/2	P.33673	—	55/33 (c)
P.33592	—	55/4	P.33678	—	55/33 (c)
P.33597	—	55/6	P.33683	—	55/33 (c)
P.33610	—	55/12	P.48672	—	63/3
P.33612	—	55/14	P.48674	—	63/3
P.33613	—	55/15	P.48675	—	63/66
P.33618	—	55/15	P.48676	—	63/66
P.33629	—	55/19 (b)	P.50219	—	63/60

Specimen	Locality
P.50248 —	63/66
P.50249 —	63/66
P.50252 —	63/68
P.50262 —	63/70
P.50323 —	63/83
P.50335 —	63/88 (f)
P.50345 —	63/3
P.50346 —	63/3
P.50347 —	63/3
P.50357 —	63/7
P.50364 —	63/11
P.50367 —	63/12 (e)
P.50378 —	63/13
P.50382 —	63/14
P.50389 —	63/16
P.50408 —	63/24
P.50416 —	63/25
P.50443 —	63/41
P.50508 —	63/58 (d)
P.51644 —	55/26
P.53260 —	55/33 (c)

All specimens are from the *S. yassensis* Limestone except:

(a). ? From Cavan Bluff Limestone.
(b). From Bloomfield Limestone.
(c). From Bloomfield-*Receptaculites* boundary.
(d). From *Receptaculites* or Warroo Limestones.
(e). From Warroo Limestone.
(f). From Warroo or Crinoidal Limestone.

* * * * * * *

(g). Collected and presented by Mr. A. J. Shearsby.
(h). Collected and presented by Mr. D. J. Cameron.

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EXPLANATION OF LETTERING IN FIGURES

ADL	anterior dorsolateral plate
ad.n.cav	anterior depression (division) of nasal cavities
afcv	anterior fenestra of neurocranial cavity
ahm	articular surface (unossified) for hyomandibula
AL	anterior lateral plate (dorsal cleithral plate)
ALap	apron of *AL*
am.eth.sh	anterior margin of ethmoid shield
a.on + v.on	canal for the orbito-nasal artery and vein
arAL	area on *PNu* and *PM* overridden by *ADL* and *AL* (Stensiö's 'Sub-obstantic area)
arEsc	areas on both *PNu* + *Nu* and *ADL* overridden by extrascapular plate
arSO	area overridden by SO chiefly on *PtO*
aup	seating of autopalatine part of palatoquadrate on inner face of *SO*
AVL	anterior ventrolateral plate
avs	anterior ventral sulcus
b.V2	foramen or arch for the passage forwards of the lateral buccal and maxillary nerves
C	central plate
Cp.hyp.v	capsule of *fo.hyp.v* (extension of parasphenoid)
csc	central sensory canal
c.tel	cavity for telencephalon (and olfactory lobes)
c.v	cranial cavity
cr.pr	intermuscular or carinal process of *MD*
d.end	external aperture of endolymphatic duct
d.end.i	internal aperture of endolymphatic duct
dg	dorsal groove for vessels to *iws*
dls	dorso-lateral space for vessels to *iws*
dpmcu	cucullaris depression
dt	dermal tubercles inside nasal cavity
ehy	groove for efferent hyoid artery
Epio	epiotic prominence
eth.sh	ethmoidal shield (imperfect in fig. 8)
fbha	anterior, bilobate buccohypophysial foramina
fbhp	? posterior buccohypophysial foramen
fe.hyp.	fenestra hypophyseos in ventral endocranial wall
flv	levator pit for insertion of levator muscle of head
f.m	foramen magnum
fno	canals of subdivided olfactory nerve (I)
f.nv	orbito-ethmoidal foramen or slit (*sl.oe*, Stensiö 9163 : 206, fig. 72*B*, etc.)
fo.hyp.v	inferior division of fossa hypophyseos situated between *Psph* and endocranium
fsp	sub-pituitary fenestra
gc	glenoid condyle (articular trochlea of post-temporal plate of Stensiö 1963, etc.)
gda	groove for dorsal aorta
gf	glenoid fossa (lateral articular fossa of Stensiö 1963, etc.)
gp	glenoid process (occipital para-articular process of Stensiö 1963, etc.)
gra	groove for 'Rachendachhypophyse'
gr II	groove for optic nerve
hc	anterior part of supramaxillary (supra-oral) sensory line
hc 2	cheek-line (post-suborbital line)
ic	possible position of internal carotid artery
ifp	infranuchal pit
IL	interlateral plate (clavicle)
ILap	apron of IL

inr	median infranuchal ridge
ioc	infraorbital sensory canal
iw	internasal wall
iws	internasal wall-space
IXph	canal for pharyngeal branch of IX
ke	median keel under MD
lac	'accessory twig' sensory line
lcvl	ventrolateral sensory line
ld	dorsal branch of main lateral line canal
lv	lateral hypophysial vein
M	marginal plate
m.cd	dorsal attachment scars of m. constrictor dorsalis
m.chy	dorsal attachment scars of m. constrictor hyoides and possibly also for m. adductor mandibulae
mlc	main lateral line canal
mp	middle pit-line groove
MD	median dorsal plate
nda	naturally decayed areas
nmv	naso-maxillary vein
noe	position of exhalent nostril
noi	position of inhalent nostril
Nu	nuchal plate
oaADL	area under *MD* overlapping *ADL*
oAL	area overlapped by *AL*
oAMV	area of *IL* overlapping anterior median ventral plate
oAVL	area of *IL* and *Sp* overlapped by *AVL*
oaPDL	area under *MD* overlapping *PDL*
occ	occipital cross-commissural sensory line
oMD	area overlapped by *MD*
oNu	area overlapped by *Nu*
oph.l	lateral ophthalmic nerve canal
oph.V	superficial ophthalmic nerve canal
oPL	area overlapped by *PL*
orb	orbit
pcv	posterior cerebral veins
pi	probable position of pineal opening
pd.n.cav	posterior depression of nasal cavity
pfSp	posterior face of *Sp*
plae	posterolateral angle of endocranium (=supravagal process and craniospinal process in coccosteids)
p.lat.pr	posterior lateral process of subnasal shelf
PM	postmarginal plate
pmc	postmarginal sensory canal
pnw	posterior face of postnasal wall
PNu	paranuchal plate
pp	posterior pit-line groove
pq.m	seating of middle part of palatoquadrate on inner face of *SO*
PrO	preorbital plate
prpoa	anterior postorbital process
prpop	posterior postorbital process
pr.pvl	posteroventral palatine process
psba	canal of efferent pseudobranchial artery
Psph	parasphenoid
pt.my	posterior myodome

PtO	postorbital plate
pt.si	sinus of pituitary vein
p.V2,3	passage for maxillary and mandibular nerves
rcr	roof of cranial cavity at fenestra
rcv	roof of cranial cavity
r.la.c	remains of labyrinth cavity
RP	rostro-pineal plate
rpto	postorbital ridge
sb.sh	sub-orbital shelf
ScCo	scapulocoracoid
sgp	sub-glenoid process
shy	canal for hyoid vein
sns	sub-nasal shelf
SO	suborbital plate
SOa	articular head for *SO*
soc	supraorbital sensory canal
soPF	socket for pectoral fin (pectoral fenestra)
sos	supraoccipital spine
Sp	spinal plate
spio	canals of spino-occipital nerves
th.n	endolymphatic thickening
u.end	undersurface of endocranium
uScCo	inner surface of perichondral cover of coracoid process with canals for dorsal cutaneous nerves and vessels
V2,3	profundus canal
vca	anterior cerebral vein
vcr	vessels to cranial roof complex
vdm	canal for vein on posterior face of occipital region
VI	abducens canal
VIIhm	hyomandibular branch of facialis canal
vju	canal for jugular vein
vju.p	posterior aperture of canal for jugular vein
vmh	median hypophysial vein
v.on	orbito-nasal vein
vrm	veins draining roof of mouth
vse	ventral surface of endocranium
X	vagus canal
X_1	canal for first branchial trunk of vagus nerve
$X_?$	canal for second branch of vagus or the post-cerebral vein

PLATE 1

Parabuchanosteus murrumbidgeensis (White)

Fig. 1. Underside of skull-roof with parasphenoid. P.48672—slightly reduced. Most of the 'canals' seem to be *post mortem* worm tubes.

Fig. 2. Flattened skull-roof with outlines of component bones painted in. P.33592—slightly reduced. See Text-fig. 3.

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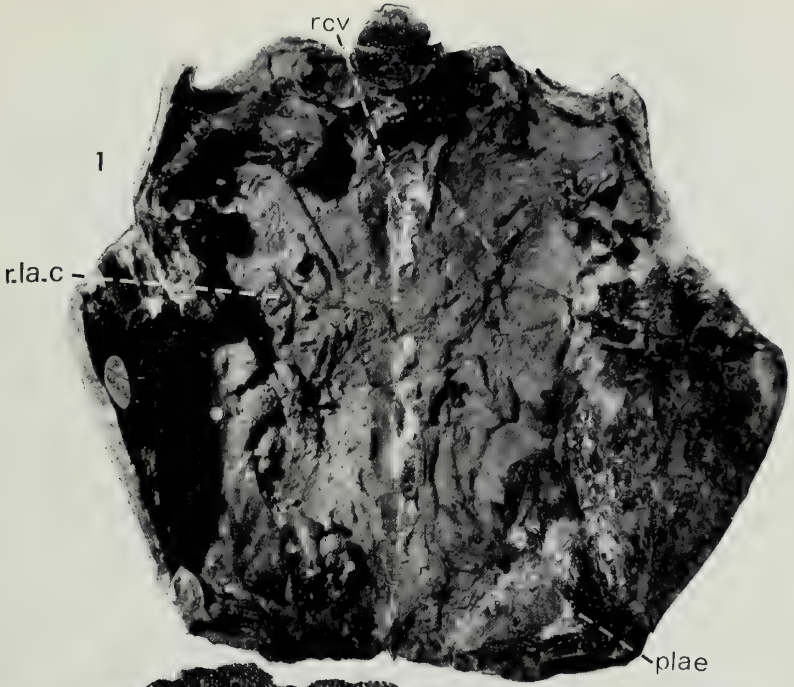
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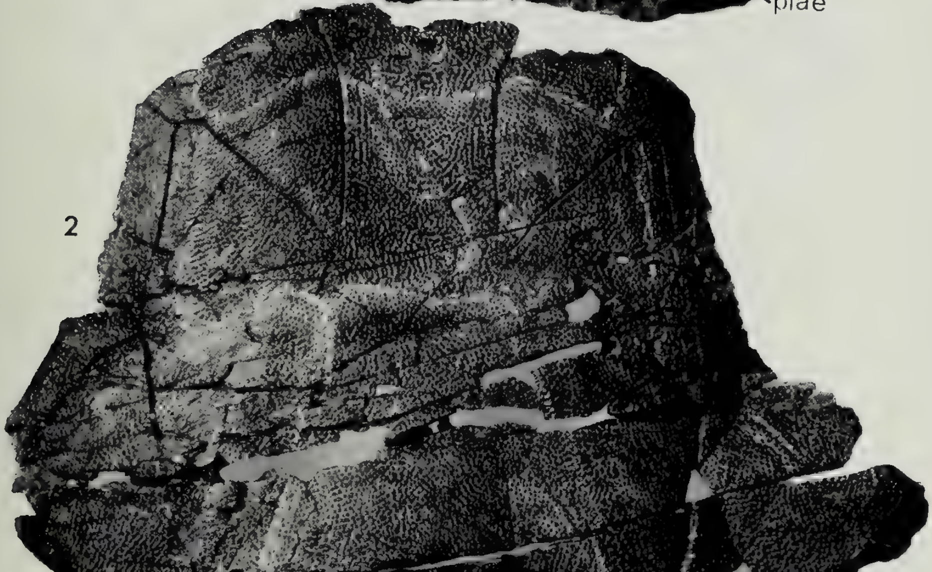

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PLATE 2

Parabuchanosteus murrumbidgeensis (White)

FIG. 1. Right anterior half of fragmentary endocranium in side view, tilted upwards. P.48675 × $1\frac{1}{2}$ approx. For explanation see Text-fig. 11; cf. Plate 4.

FIG. 2. Front view of same specimen. × $1\frac{2}{3}$ For explanation see Text-figs 8, 9.

FIG. 3. Skull-roof of same specimen, lit from behind. Nat. size. *Cf.* Text-fig. 3.

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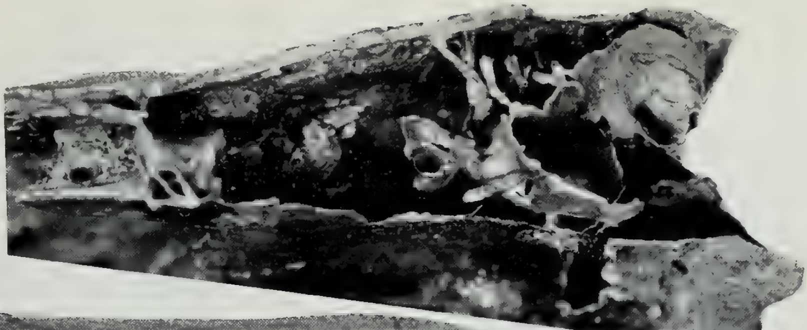

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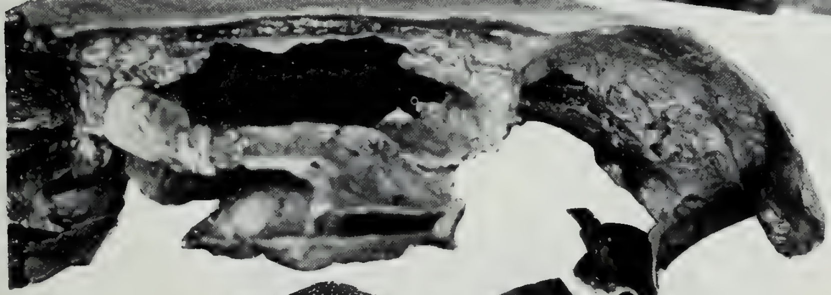

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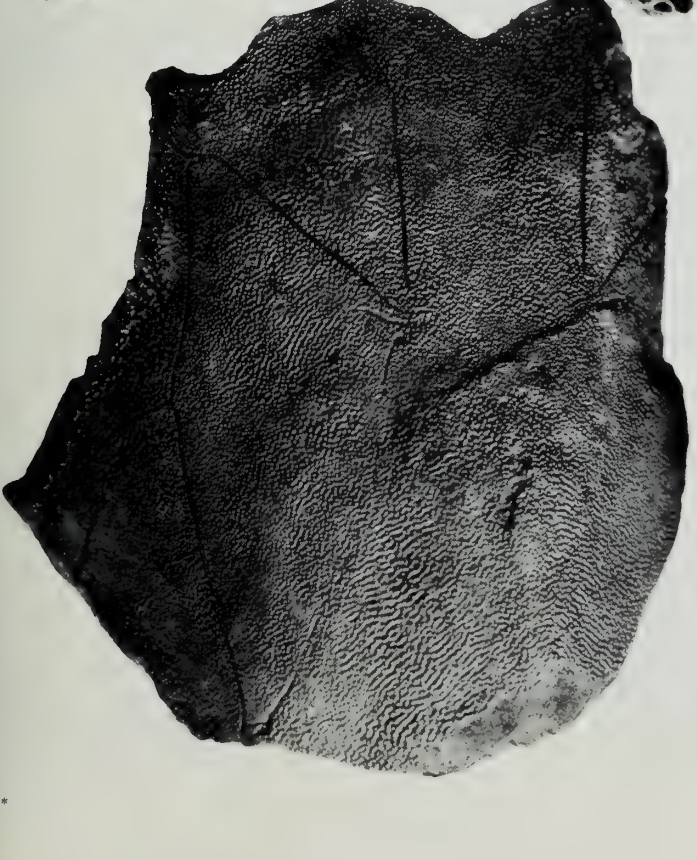
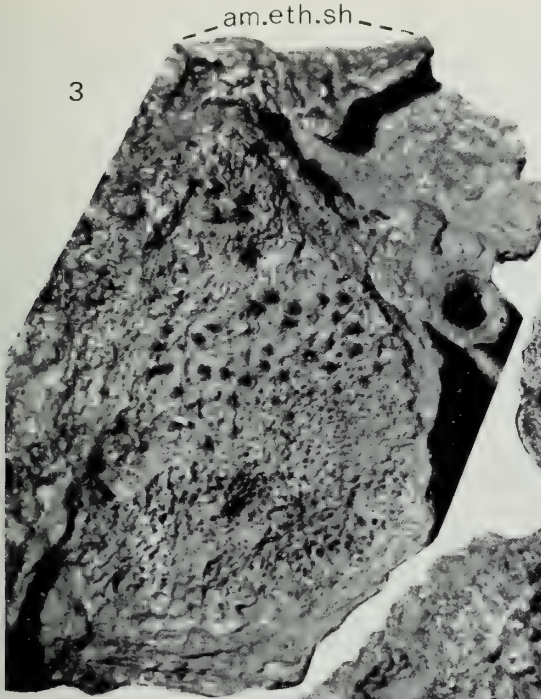


PLATE 3

Parabuchanosteus murrumbidgeensis (White)

Figs 1–3. Three parasphenoids in varying states of resorption or decay. ×4½. explanation see Text-figs 5–7.

3



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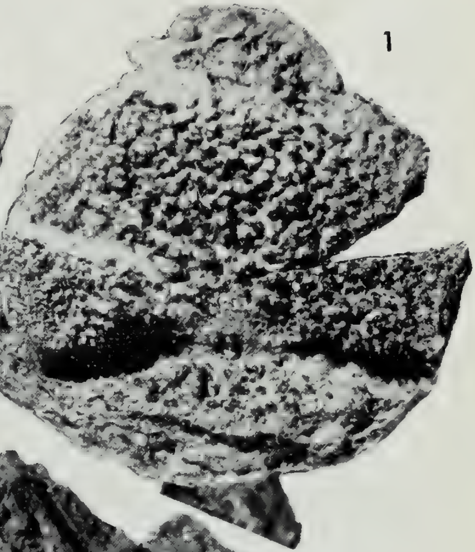

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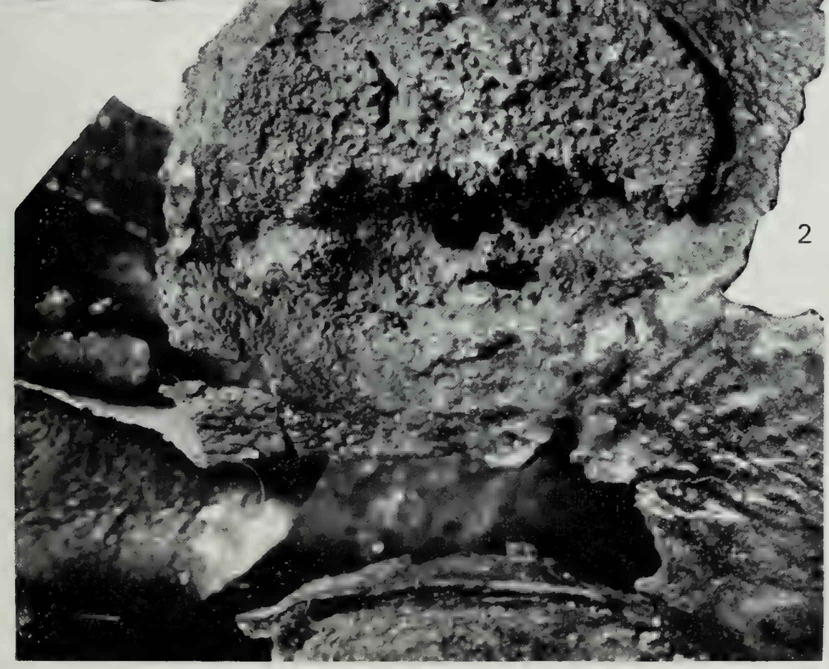

PLATE 4

Parabuchanosteus murrumbidgeensis (White)

Ventral view of imperfect skull, re-touched P.48675 × $1\frac{1}{2}$. For explanation see Text-fig. 4. (Same specimen as in Plate 2 & Plate 3, fig. 2).

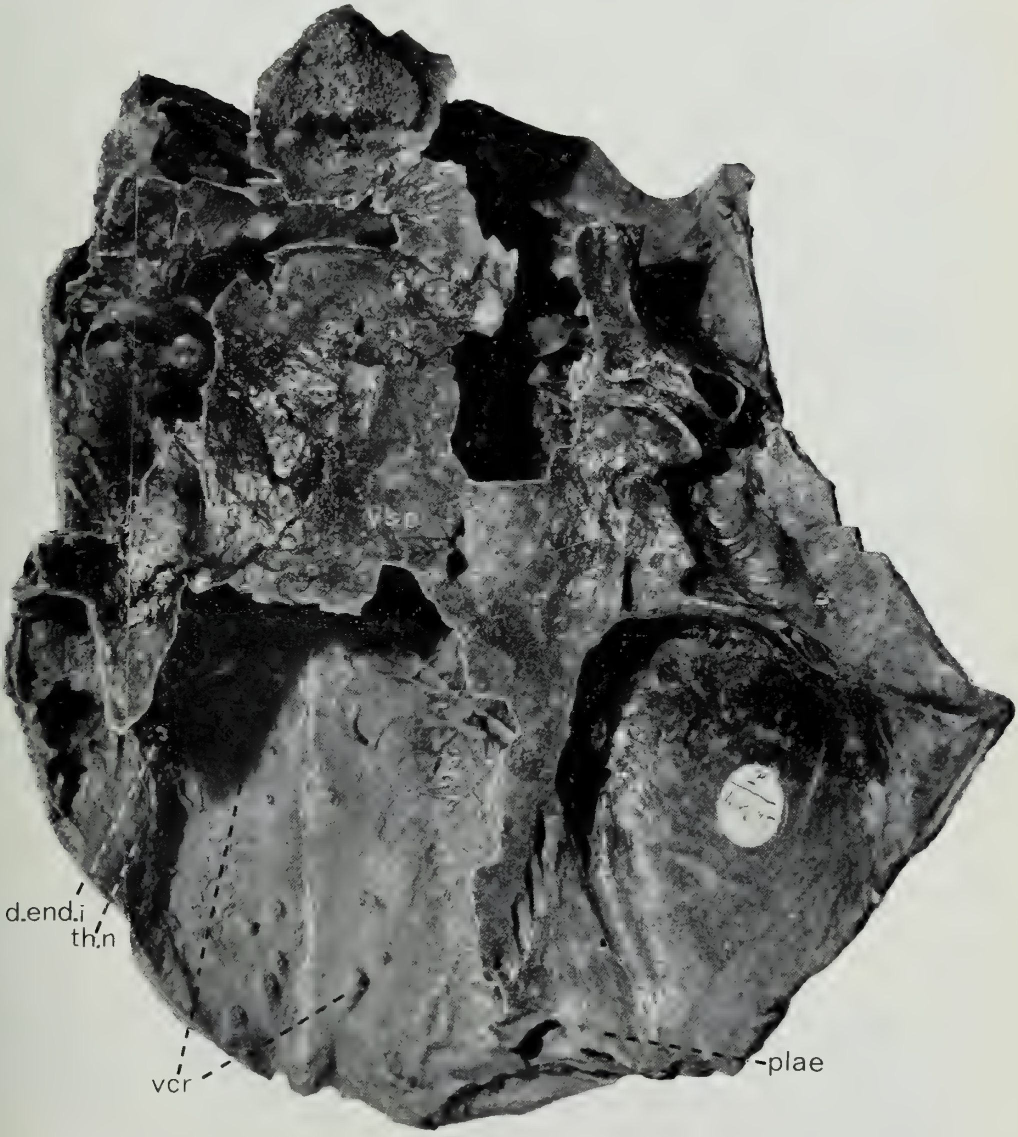
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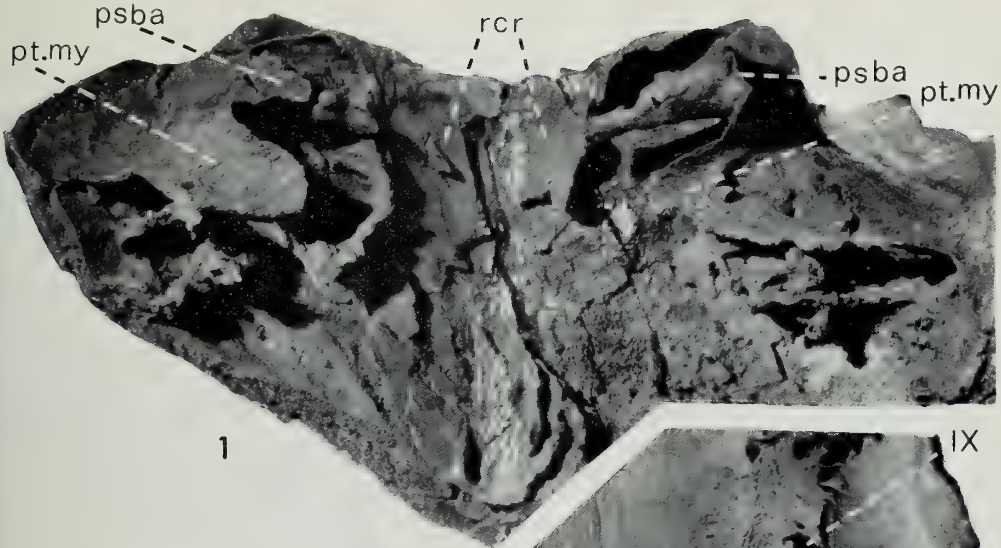
PLATE 5

Parabuchanosteus murrumbidgeensis (White)

FIG. 1. Anterior end of skull-roof from below, with most of endocranium missing. P.48674 × 2.

FIG. 2. Posterior end of ventral surface of endocranium shewing foramina and canals of spino-occipital nerves, etc. P.33597 × 1½. *Cf.* Text-fig. 4 and Pl. 4.

FIG. 3. Same specimen. Posterior margin of dorsal surface of skull-roof shewing sensory canals and pit-lines. × 2.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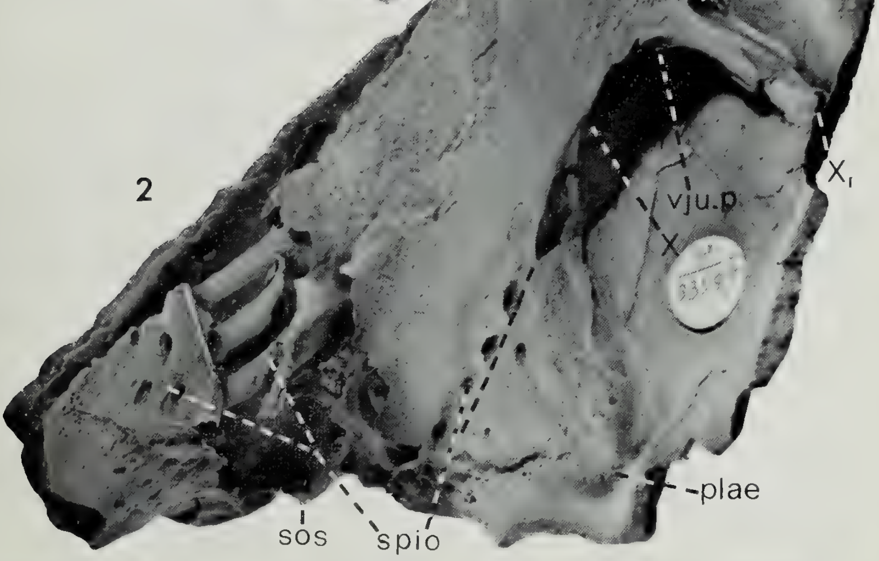
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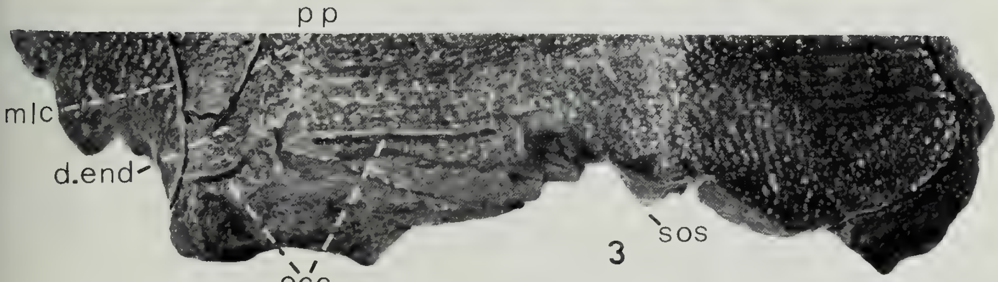
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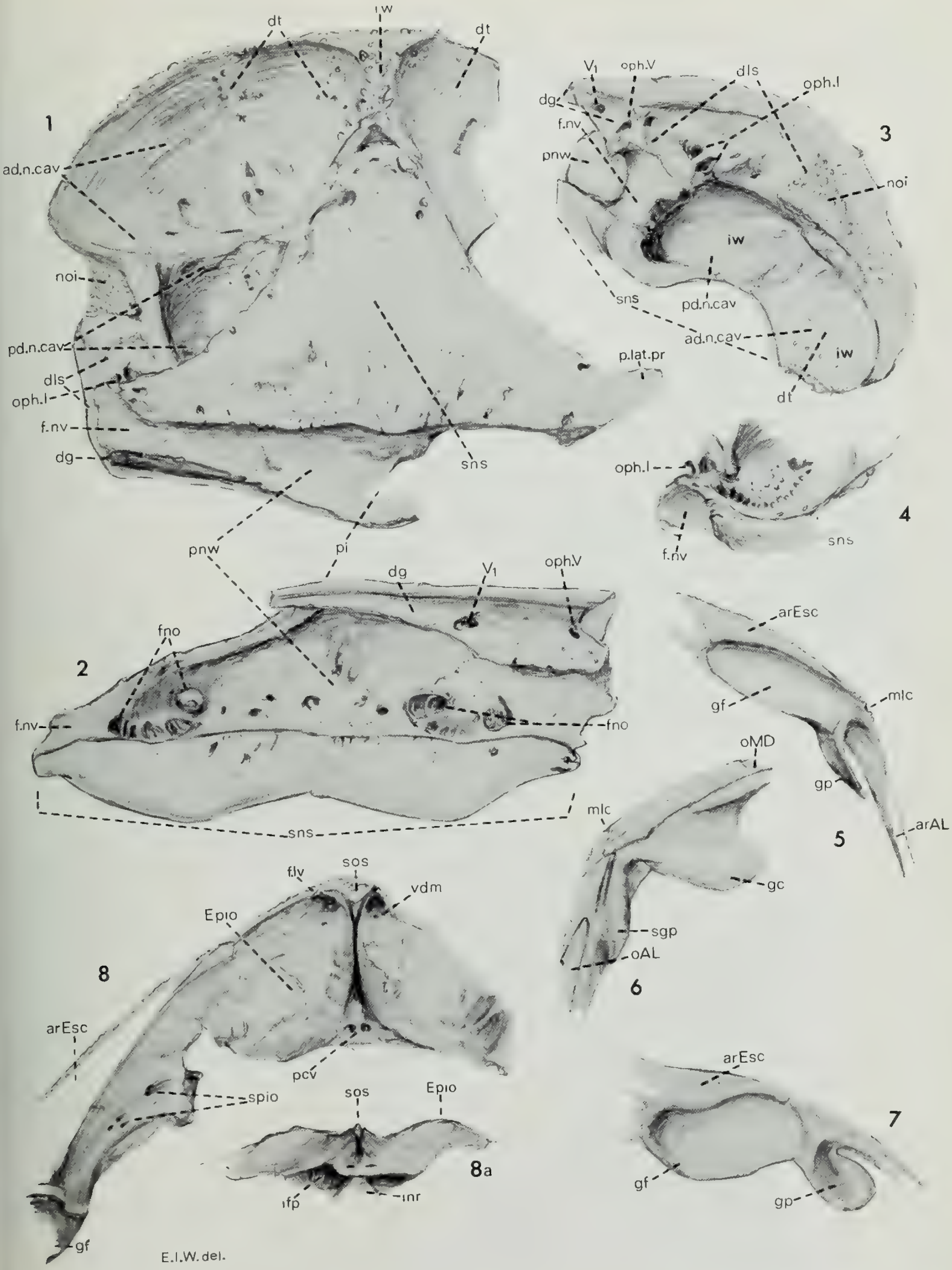
PLATE 6

Parabuchanosteus murrumbidgeensis (White)

FIG. 1. Rostro-pineal bone, ventral view. P.33612 × 2¼ approx.
FIG. 2. Same, posterior view.
FIG. 3. Same, right side.
FIG. 4. Same, right cribrosal area of post-nasal wall seen from front ×2.
FIGS 5, 6. Associated imperfect right paranuchal plate (posterior view) and anterior lateral plate (anterior view)—see also Pl. 7. P.33683 A, B × 1½.
FIG. 7. Right paranuchal articulation. P.33610 × 1⅘.
FIG. 8. Posterior view of skull. *8a*, Median occipital area seen from below. P.48676 × 2½. For explanation see Text-fig. 2.

PLATE 6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E.I.W. del.

PLATE 7

Parabuchanosteus murrumbidgeensis (White)

FIGS 1, 2. Associated imperfect right paranuchal plate and anterior dorsolateral plate to shew articulation. P.33683 *A*, *B* × 2. See also Pl. 6, figs 5, 6.

FIGS 3, 4. The same, undersurface.

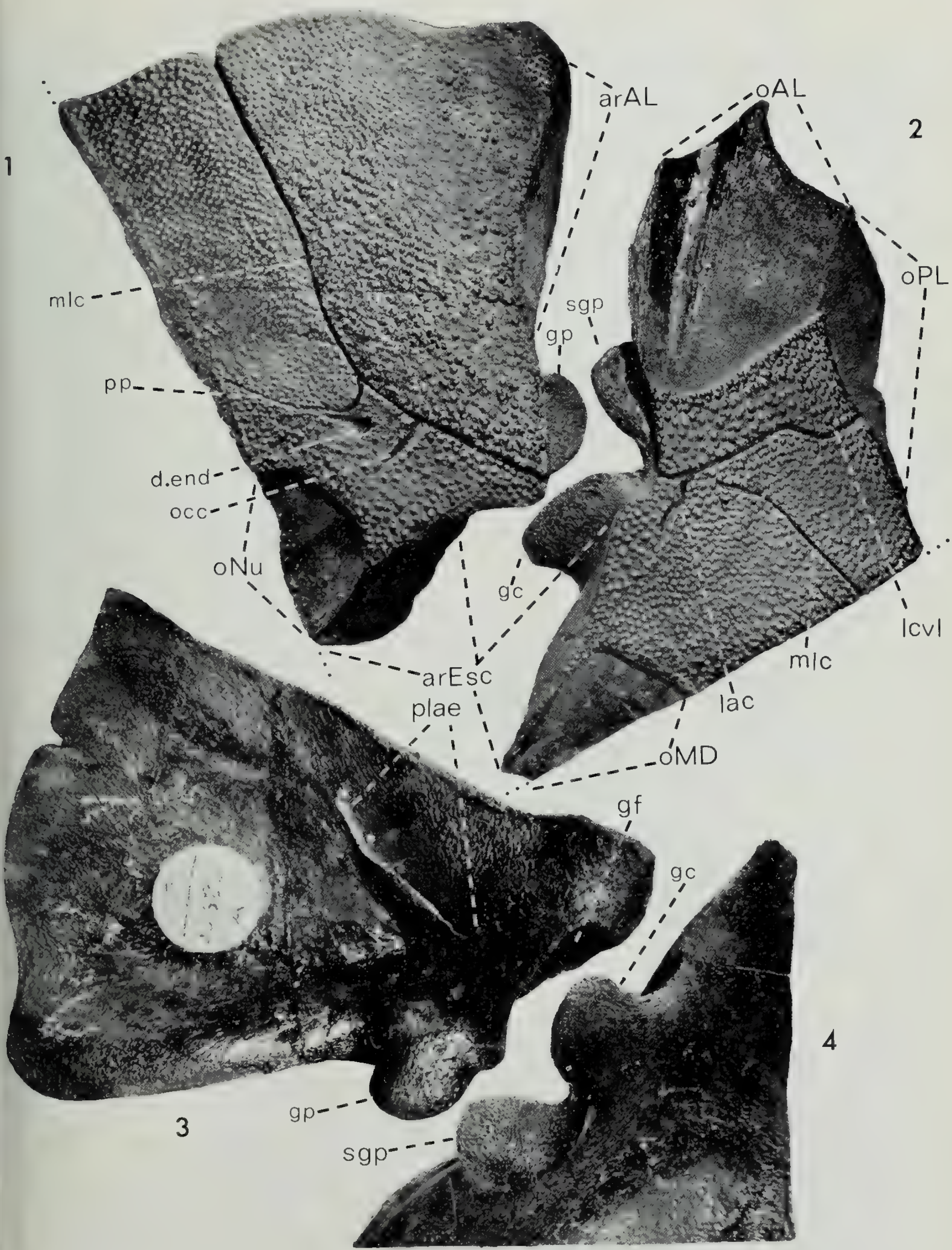
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PLATE 8

Parabuchanosteus murrumbidgeensis (White)

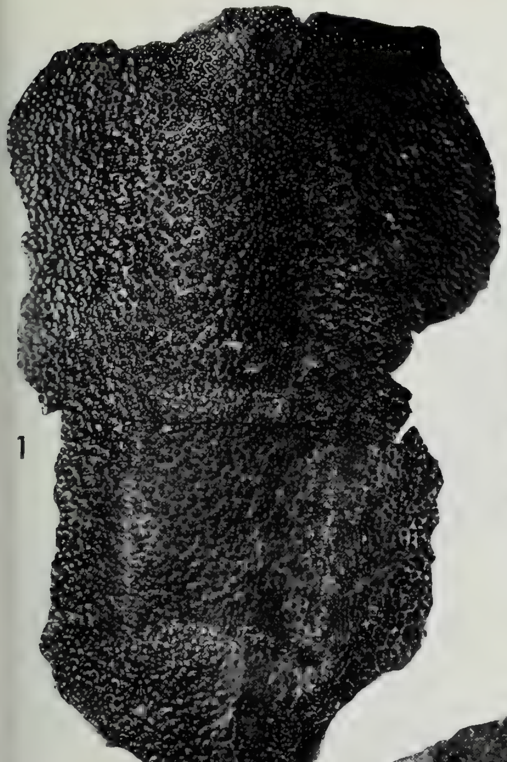
FIG. 1. Imperfect median dorsal plate, P.50347 × $1\frac{1}{2}$.

FIG. 2. Imperfect median dorsal plate, ventral view. P.33583 × $1\frac{1}{2}$. See Text-fig. 17.

FIG. 3. Imperfect right suborbital plate. P.50416 × $1\frac{1}{2}$. See Text-fig. 14.

FIG. 4. Lower half of left anterior lateral plate shewing upper part of apron and spinal margin. P.50248 × $1\frac{1}{2}$. See Text-fig. 18.

FIG. 5. Part of ornamentation of Fig. 1 × 10.



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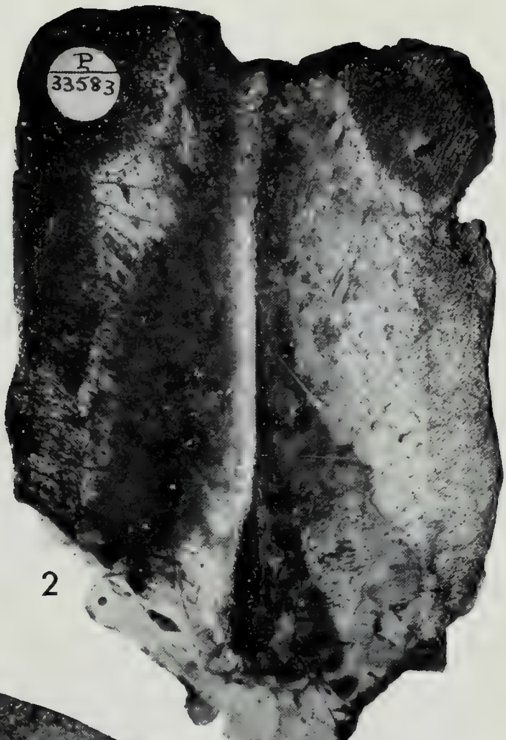

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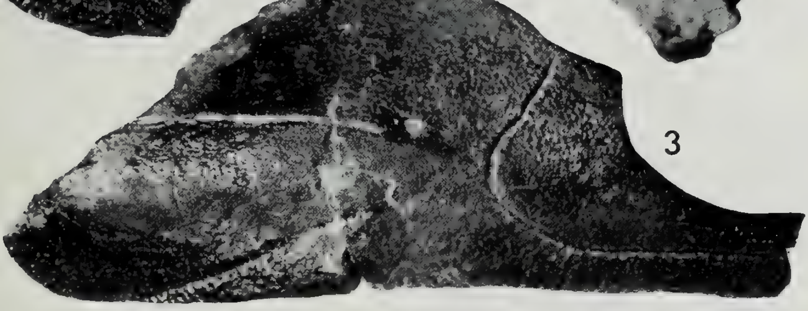

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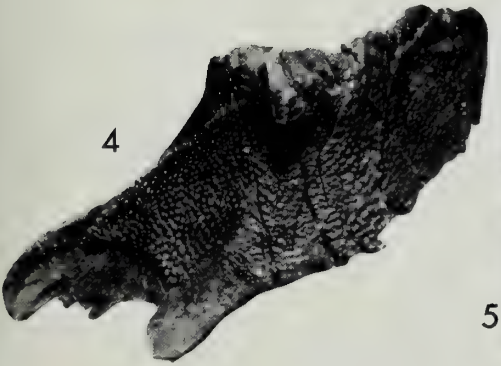

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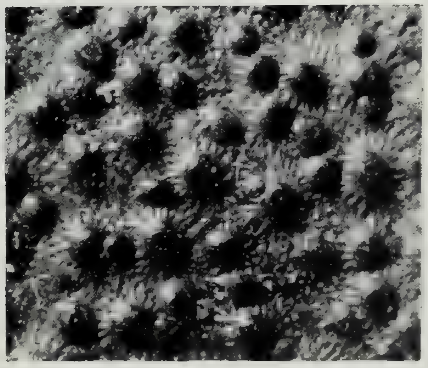

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PLATE 9

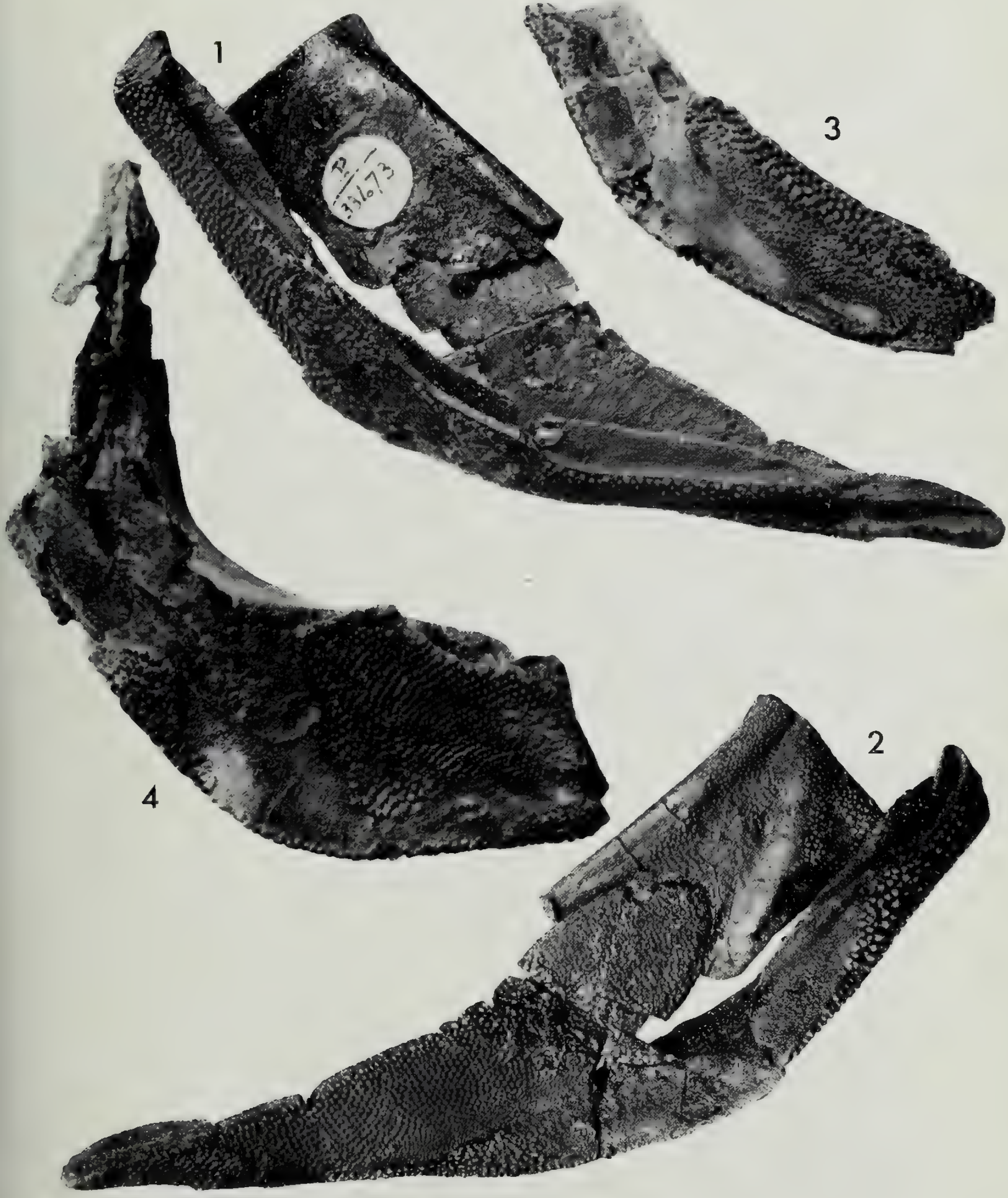
Parabuchanosteus murrumbidgeensis (White)

Fig. 1. Underside of left interlateral and spinal plates and apron of anterior lateral. P. 33673 × 1⅓.

Fig. 2. Upper surface of same specimen.

Fig. 3. Part of right interlateral plate shewing unworn denticular ornamentation with fragment of spinal plate attached. P.50323 × 1⅓.

Fig. 4. Part of large interlateral plate with complete spinal plate and much of scapulocoracoid and articular surface. P.50378 × 1⅓.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PLANKTONIC FORAMINIFERA FROM THE PALAEOCENE-EOCENE SUCCESSION IN THE RAKHI NALA, SULAIMAN RANGE, PAKISTAN

B. K. SAMANTA

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 6
LONDON : 1973

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ATURAL H

PLANKTONIC FORAMINIFERA FROM THE PALAEOCENE-EOCENE SUCCESSION IN THE RAKHI NALA, SULAIMAN RANGE, PAKISTAN

BY
BIMAL KUMAR SAMANTA
University of Calcutta

Pp. 421–482; 15 *Plates,* 3 *Text-figures,* 2 *Tables*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 6
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PLANKTONIC FORAMINIFERA FROM THE PALAEOCENE-EOCENE SUCCESSION IN THE RAKHI NALA, SULAIMAN RANGE, PAKISTAN

By B. K. SAMANTA

SYNOPSIS

The Palaeocene-Eocene succession exposed in the Rakhi Nala section, Sulaiman Range, Pakistan is made up of four formations, in ascending order the Ranikot, Dunghan, Ghazij and Khirthar. About one hundred and twenty samples from this sequence were examined for planktonic foraminifera. None was recognized in the Ranikot Formation, in the lower part of the Dunghan Formation or in the upper part of the lower Khirthar Formation. The upper part of the Dunghan Formation, the lower part of the Ghazij Formation and the upper part of the Khirthar Formation contain good autochthonous planktonic foraminifera. In contrast, the upper part of the Ghazij Formation and the lower part of the lower Khirthar Formation yielded only reworked Upper Cretaceous forms.

A total of seventy-nine species and subspecies of foraminifera belonging to ten genera are discussed and figured. Two are described as new. Eight zones are recognized from the base upwards: the *Globorotalia angulata* Zone, the *Globorotalia velascoensis* Zone, the *Globorotalia aequa* Zone, the *Globorotalia formosa formosa* Zone, the *Globorotalia aspensis/Globorotalia esnaensis* Zone, the *Globorotalia crassata/Truncorotaloides topilensis* Zone, the *Truncorotaloides rohri* Zone and the *Globigerina officinalis* Zone. The lower three zones are assigned to the Palaeocene and the two succeeding zones to the Lower Eocene. Of the remaining three zones, two are assigned to the Middle Eocene and one to the Upper Eocene. The upper part of the Dunghan Formation is here dated as Middle Palaeocene to early Lower Eocene, the lower part of the Ghazij Formation as middle Lower Eocene and the upper part of the Khirthar Formation as late Middle Eocene to Upper Eocene.

INTRODUCTION AND ACKNOWLEDGEMENTS

The fossiliferous marine sequence exposed in the Rakhi Nala, a river in the Sulaiman Range, Western Punjab, Pakistan, has attracted the attention of geologists mainly because of its accessibility and good exposures. Eames' (1952*b*, *c*) detailed account of the Rakhi Nala section, based on the observations made by geologists of the Burmah Oil Company, revealed that the succession there extends from the Cretaceous to the Upper Eocene. In his biostratigraphical paper (1952*c* : 174) he considered all the fossils, except the smaller foraminifera and ostracods, recovered from the Palaeocene-Eocene part of the sequence. However, only the molluscan fauna from the Rakhi Nala succession was treated systematically (Eames 1951, 1952*a*).

During the 1956–57 field season, Dr D. D. Bayliss visited the Rakhi Nala section with geologists of the Standard Vacuum Oil Company, and systematically collected two hundred and sixty five samples through the Lower Tertiary part of the sequence.

The larger foraminifera from these samples were described by Bayliss (1961 : unpublished thesis). Latif (1961)* listed the planktonic foraminifera from the same residues and commented on their ranges.

This paper, the main objects of which are the description and illustration of the plankton and the zonation of the Palaeocene-Eocene part of the Rakhi Nala sequence, is based on a study of Bayliss' original samples, now deposited in the Department of Geology, University College of Wales, Aberystwyth. The stratigraphy and larger foraminifera will be described separately in a joint paper with Dr Bayliss.

The writer is greatly indebted to Dr J. R. Haynes of the Geology Department of the University College of Wales, Aberystwyth for making available the material for the present study, for help, advice, and for critically reading the manuscript; to Professor Alan Wood for providing facilities in the Geology Department at Aberystwyth; to Dr C. G. Adams of the British Museum (Natural History), London, for valuable suggestions and for access to the collections in his care; to Dr D. D. Bayliss, lately of the British Museum (Natural History) for much help and useful discussions and to Dr F. E. Eames for helpful correspondence and discussions on the Palaeocene-Eocene biostratigraphy of the Indian region. Thanks are also due to Dr C. L. Forbes (Sedgwick Museum, Cambridge) and to Professor H. M. Bolli (of the Swiss Federal Institute of Technology, Zürich), for access to collections and for helpful discussions.

STRATIGRAPHY AND MATERIAL

The Palaeocene-Eocene succession exposed in the Rakhi Nala valley is summarized in Table 1. It comprises in ascending order the Ranikot, Dunghan, Ghazij, and Khirthar Formations. The sequence, about 7130 feet thick is apparently conformable throughout, and rests conformably on the Pab formation which is usually regarded as Upper Cretaceous in age. It is overlain by an unfossiliferous sandstone unit questionably assigned to the Siwalik group. The succession is dominantly argillaceous with beds of limestone and marls at several horizons. Gypsiferous layers occur at some levels and it is sandy towards the base.

The hard, compact limestone samples were examined only in thin sections. The shale, mudstone and marl samples were disaggregated by boiling in water with washing soda for several hours, the residue then being washed through a 200 mesh sieve. When necessary the procedure was repeated several times to obtain completely matrix-free specimens. One hundred and twenty samples were processed in this way.

The illustrations are shaded camera lucida drawings by the writer.

PLANKTONIC FORAMINIFERA

The samples from the Ranikot Formation did not yield determinable foraminifera (see Table 1). Only the uppermost 384 feet of the Dunghan Formation contained satisfactorily preserved, determinable plankton, which proved to be rare to abundant in this part of the succession.

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* Latif's results are not further considered here as he appears to have illustrated at least part of his paper with figures taken from Bolli's (1957) work on the faunas of Trinidad.

Planktonic foraminifera are rare to common in the Ghazij Formation, preservation

FORMATION		SAMPLE NUMBER	THICKNESS IN FEET	LITHOLOGY	PLANKTONIC FORAMINIFERA
Khirthar	Upper	3666 3603	959	Predominantly shales and mudstones gypsiferous at places; a few layers of marls and limestones.	Samples 3665 & 3666: no planktonic foraminifera. Samples 3650 to 3664: rare to common well preserved planktonic foraminifera. Samples 3627 to 3647: very rare and poorly preserved planktonic foraminifera. Samples 3603 to 3626: common to abundant, well preserved planktonic foraminifera.
	Lower	3602 3453	1253	Mainly limestones and shales with some mudstones at places; shales gypsiferous at places and a thick massive gypsum bed.	Samples 3498 & 3499: very rare, poorly preserved, indeterminable planktonic foraminifera. Samples 3465 to 3497: no planktonic foraminifera recognised. Samples 3453 to 3464: rare to frequent, reworked planktonic foraminifera.
Ghazij		3452 3140	3607	Mainly shales and siltstones with thin bands of limestones near the top.	Samples 3199 to 3452: Rare to frequent, reworked planktonic foraminifera. Samples 3140 to 3195: rare to common planktonic foraminifera; preservation poor to satisfactory.
Dunghan	Upper	3667 3125	384	Alternations of mudstones and shales with few thin bands of fine grained sandstones in the lower part and a hard limestone bed at the top.	Rare to abundant planktonic foraminifera; preservation poor to satisfactory.
	Lower	3124 3116	375	Alternations of fine grained sandstones and shales.	No determinable planktonic foraminifera.
Ranikot		3115 3110	553	Dominantly ferruginous sandstone, conglomeratic and cross bedded in the upper part, and with a few shaly layers in the lower part.	No determinable planktonic foraminifera.

TABLE 1—The Palaeocene-Eocene succession exposed in the Rakhi Nala, Sulaiman Range, Pakistan and its planktonic foraminiferal content.

varying from poor to fairly satisfactory. In the upper 920 feet only reworked Upper Cretaceous plankton was found.

The lowest 280 feet of the Khirthar Formation also contains only rare reworked Upper Cretaceous foraminifera. In the succeeding 918 feet no planktonic foraminifera were recognized. In the uppermost 55 feet of the lower Khirthar very rare, poorly preserved and indeterminable foraminifera were observed.

The upper Khirthar is rich in planktonic foraminifera and preservation in general is good. Some samples from the lower part contain the richest planktonic foraminiferal faunas in the sequence. In the samples corresponding to an interval of 350 feet in the middle of the upper Khirthar only rare and poorly preserved foraminifera were observed.

Seventy nine species and subspecies of foraminifera belonging to ten genera are identified. The distribution of these forms is shown in Text-figs 1 and 2. Two species are described as new. All species, except the two which are provisionally identified, are represented by material adequate for satisfactory identification.

Among the ten genera represented, *Globigerina* and *Globorotalia* constitute more than 80% of the total planktonic foraminiferal fauna. *Globorotalia* is the dominant genus with thirty-four species and subspecies. This genus is most abundant in the Dunghan Formation where it is represented by twenty-seven species and subspecies. The angulo-conical forms of *Globorotalia* are dominant here, but in the overlying Ghazij Formation the genus is represented by only seven species. The fauna here is dominated by coarsely ornamented forms. In the upper Khirthar, *Globorotalia* is again represented by seven species. Here, as in the Ghazij Formation, coarsely ornamented forms are dominant. This genus was not recognized in the upper part of the upper Khirthar.

Globigerina, represented by twenty-four species and subspecies, is the next most abundant genus in the sequence. It is the only genus which ranges from the base of the upper Dunghan to the top of the upper Khirthar in this succession. In the upper Dunghan Formation it is represented by ten species while in the overlying Ghazij it is represented by only two species. In the older samples from the upper part of the Dunghan Formation, reticulate forms are most numerous. In samples from the highest part of this Formation and from the Ghazij Formation, spinose forms are more common.

Globigerina becomes most abundant in the upper part of the Khirthar Formation where it is represented by fourteen species and subspecies, some of which develop very distinctive tests. Species with finely papillose and hispid surfaces are dominant.

Pseudohastigerina, which is represented by five species, appears for the first time in the uppermost part of the Dunghan Formation. It is represented by two species as in the overlying Ghazij Formation. In the upper part of the Khirthar Formation it is represented by three species and is most abundant in the middle part.

The representatives of the remaining seven genera appear for the first time in the upper part of the Khirthar Formation. The genus *Globigerinita* which is represented by four species occurring throughout. *Chiloguembelina* and *Truncorotaloides* are each represented by three species. The representatives of the former occur throughout while those of the latter are restricted to the lower part. *Globigerapsis* and

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GHAZIJ FORMATION
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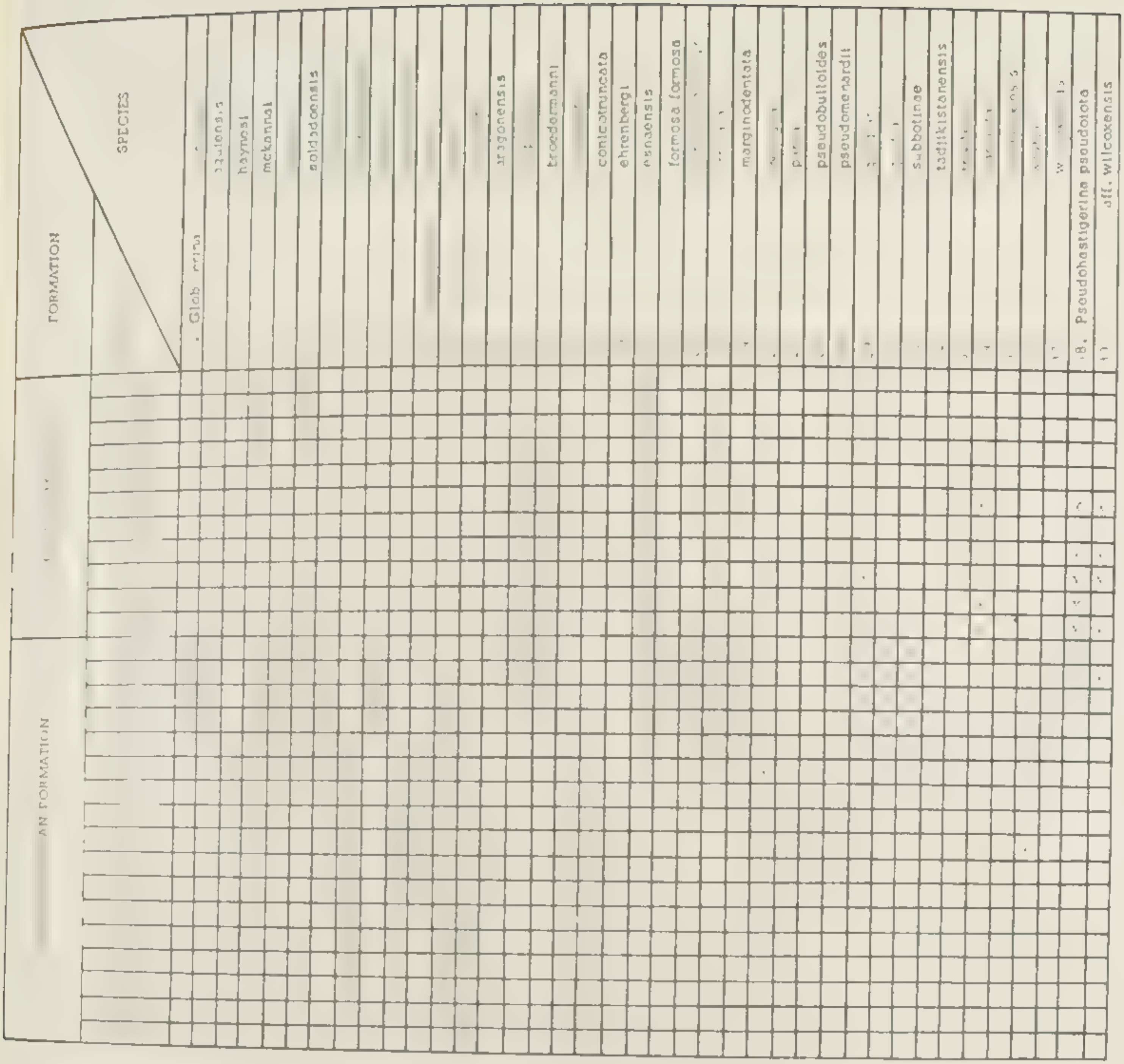

FORMATION

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soldadoensis

aragonensis

broedermanni

conicotruncata

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formosa formosa

marginodentata

pseudobulloides

pseudomenardii

subbotinae

tadjikistanensis

18. Pseudohastigerina pseudolota

aff. wilcoxensis

[illegible] in the Upper Dunghan and Ghazij Formations exposed in the Rakhi Nala section, Pakistan

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Globorotalia angulata zone

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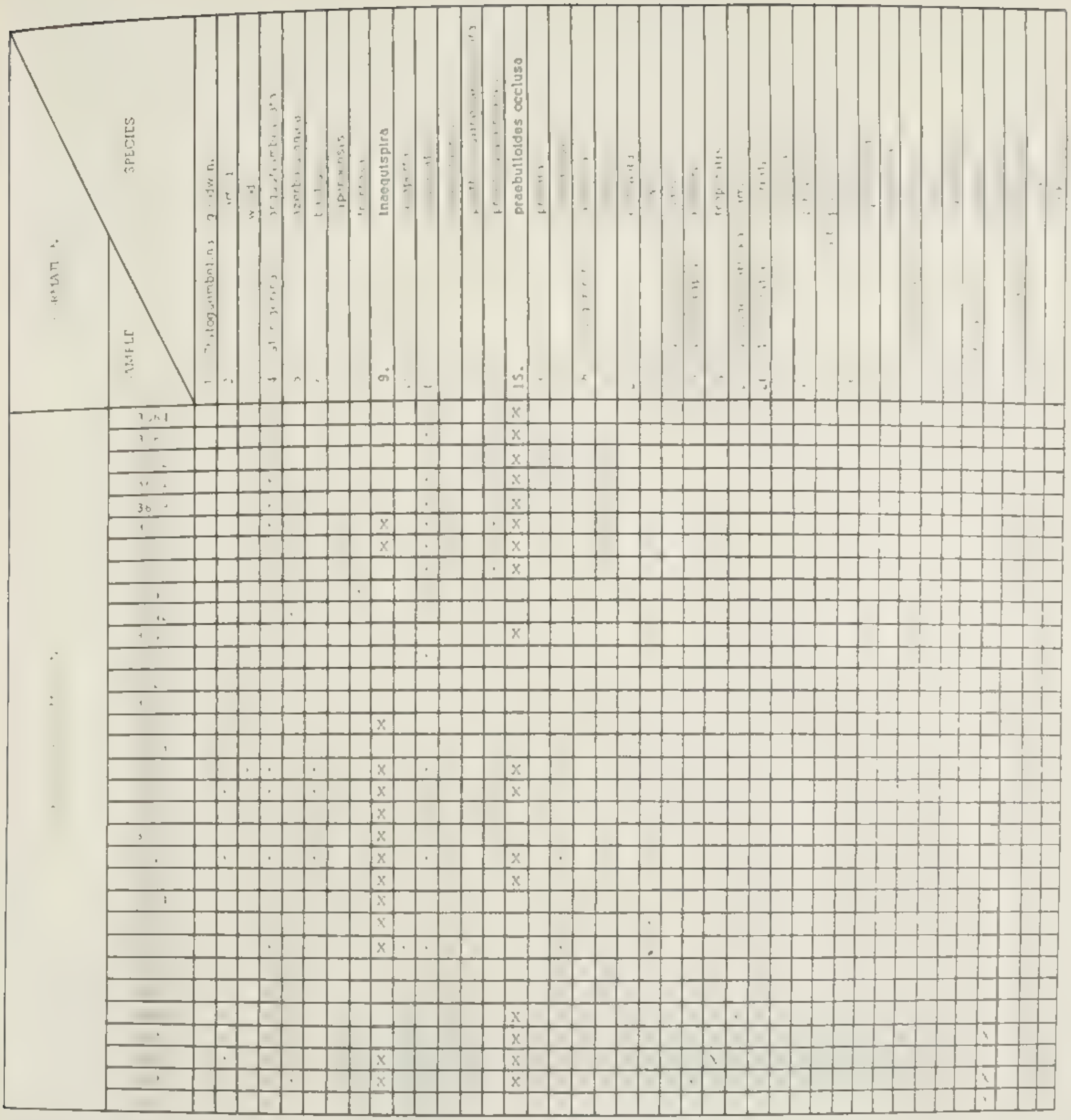
SPECIES
SAMPLE
1. [illegible]logumbelina [illegible]
9. inaequispira
15. praebuliloides occluso
36

Fi[illegible] Distribution of planktonic foraminifera in the Upper Khattar Formation [illegible] section, Pakistan

FORMATION	SAMPLE
UPPER KHIRTHAR FORMATION	36
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SPECIES

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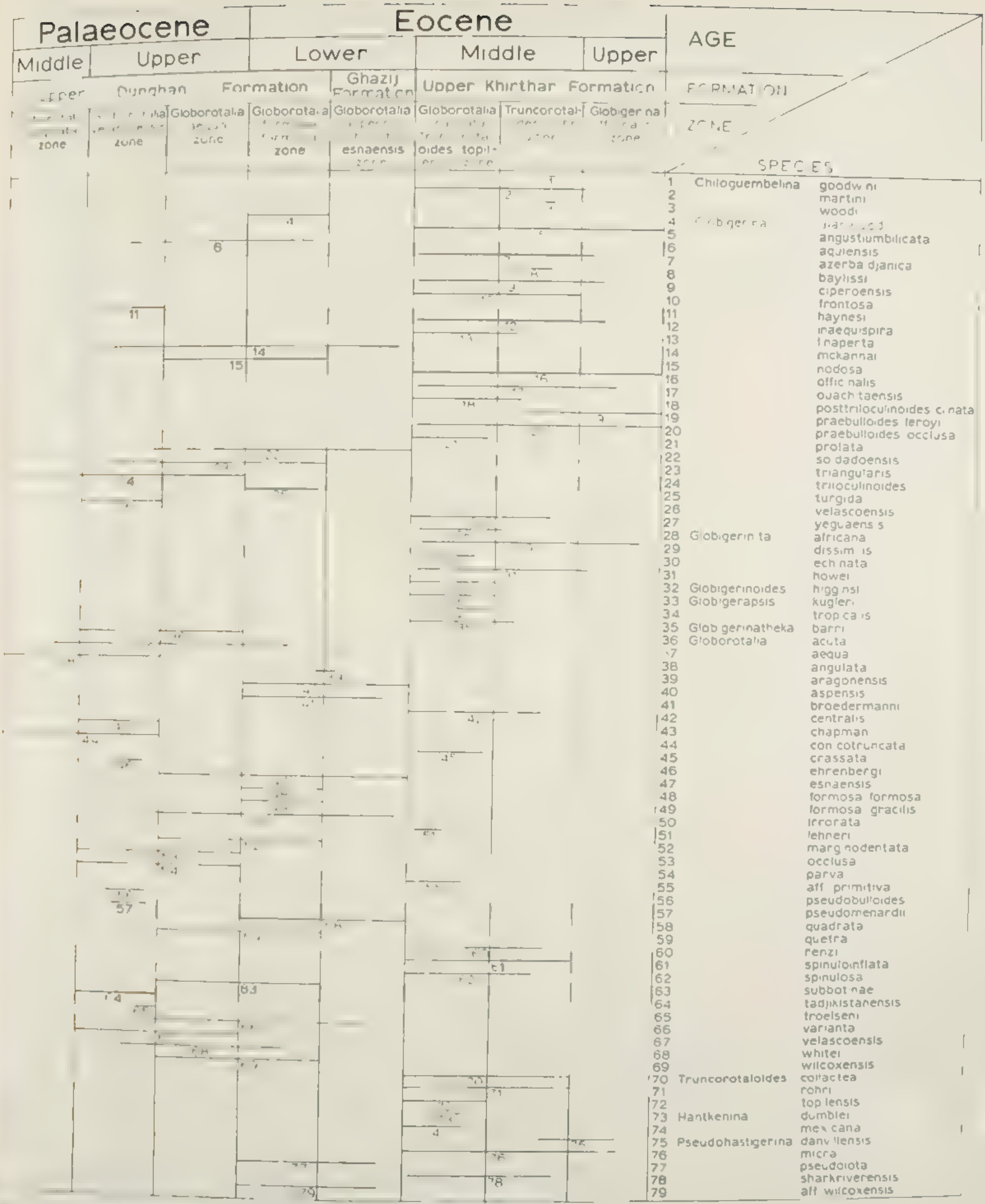

FIG 3—Stratigraphic distribution of planktonic foraminifera in the Palaeocene-Eocene succession exposed in the Rakhi Nala, Sulaiman Range, Pakistan.

Hantkenina are each represented by two species, and *Globigerinoides* and *Globigerinatheka* by one species; these four genera are restricted to the lower part of the upper Khirthar Formation. They include some of the most distinctive species in the sequence.

ZONATION AND CORRELATION

Eight faunal zones have been recognized in the sequence (Table 2, Text-fig. 3). There is an interval between the fifth and the sixth which contains reworked Upper Cretaceous foraminifera in its lower part and which lacks any identifiable planktonic foraminifera in the upper part. The eight zones are discussed below in statigraphical order.

FORMATION		PLANKTONIC FORAMINIFERAL ZONES	AGE	
Khirthar	Upper	*Globigerina officinalis* Zone	Upper	EOCENE
		Truncorotaloides rohri Zone	Middle	
		Globorotalia crassata/*Truncorotaloides topilensis* Zone		
	Lower	No determinable planktonic foraminifera in the upper part; rare, poorly preserved and reworked planktonic foraminifera in the lower part.		
Ghazij		*Globorotalia aspensis*/*Globorotalia esnaensis* Zone	Lower	
Dunghan	Upper	*Globorotalia formosa formosa* Zone		
		Globorotalia aequa Zone	Upper	PALAEOCENE
		Globorotalia velascoensis Zone		
		Globorotalia angulata Zone	Middle	
	Lower	No determinable planktonic foraminifera		

TABLE 2—Planktonic foraminiferal zonation of the Palaeocene-Eocene succession exposed in the Rakhi Nala, Sulaiman Range, Pakistan.

1. The *Globorotalia angulata* Zone

This is represented by samples 3125 to 3129 from the upper Dunghan Formation. Four species, *Globigerina triloculinoides* Plummer, *Globorotalia aequa* Cushman & Renz, *G. angulata* (White) and *G. conicotruncata* Subbotina, occur here, and of these, *G. angulata* is the most distinctive. Preservation is not very satisfactory. All four species range up into the next zone where they become more common. Immediately underlying this zone is an interval with no planktonic foraminifera.

On the basis of its foraminifera and stratigraphical position this zone is tentatively correlated with the combined *Globorotalia angulata* and *Globorotalia pusilla pusilla* Zones of Bolli (1966). It is assigned here to the Middle Palaeocene.

2. The *Globorotalia velascoensis* Zone

This is represented by samples 3130 to 3137 from the upper Dunghan formation. It is characterized by the abundance of *Globorotalia velascoensis* (Cushman) and closely related species such as *G. acuta* Toulmin, *G. occlusa* Loeblich & Tappan and *G. parva* Rey. The lower limit of the zone is marked by the first appearance of *G. velascoensis* (Cushman).

Of the twenty-three species of *Globigerina* and *Globorotalia* occurring here four range up from the *G. angulata* zone.

Among the nineteen species appearing in this zone, eight are restricted to it. They are *Globigerina haynesi* El-Naggar, *G. velascoensis* Cushman, *Globorotalia chapmani* Parr, *G. ehrenbergi* Bolli, *G. pseudobulloides* (Plummer), *G. pseudomenardii* Bolli, *G. tadjikistanensis* Bykova and *G. troelseni* Loeblich & Tappan. *Globorotalia angulata* (White) and *G. conicotruncata* Subbotina disappear at the top of the zone. Thirteen species range up in to the overlying zone. This zone is correlated with the combined *Globorotalia pseudomenardii* and *Globorotalia velascoensis* Zones of Bolli (1957*a*, 1966). It is regarded here as belonging to the lower part of the Upper Palaeocene.

3. The *Globorotalia aequa* Zone

This is represented by sample 3138 from the upper Dunghan Formation. It is characterized by the occurrence of *Globorotalia aequa* Cushman & Renz, *G. acuta* Toulmin, *G. velascoensis* (Cushman), *G. marginodentata* Subbotina, *G. subbotinae* Morozova and *G. wilcoxensis* Cushman & Ponton. This zone is marked by the first appearance of *G. marginodentata*, *G. subbotinae* and *G. wilcoxensis*, and by the disappearance of *Globorotalia acuta*, *G. occlusa*, *G. parva*, *G. velascoensis* and *Globigerina triloculinoides*.

Among the nineteen species of *Globigerina* and *Globorotalia* occurring here thirteen range up from the underlying zone and six appear for the first time. None of the species is restricted to the zone although five do not range above it. The remaining fourteen extend up into the overlying zone.

The foraminifera and stratigraphical position of this zone indicate that it is comparable to the *Globorotalia aequa* Zone as recognized by Luterbacher (1965) in the Gubbio section of Central Italy. Luterbacher correlated his *Globorotalia aequa*

Zone with the *Globorotalia rex* Zone recognized by Bolli (1957*a*) in Trinidad. The *G. aequa* Zone is here assigned to the upper part of the Upper Palaeocene.

4. The *Globorotalia formosa formosa* Zone

This is represented by samples 3672 to 3669 from the upper part of the Dunghan Formation. It is characterized by the first appearance of the planispiral genus *Pseudohastigerina* Banner & Blow, and by the occurrence of *Globorotalia formosa formosa* Bolli and *G. formosa gracilis* Bolli. Its upper limit is marked by the disappearance of the two last-mentioned subspecies together with *G. marginodentata* and *G. subbotinae.*

Of the twenty-four species and subspecies occurring here, fourteen range up from the underlying zone. Four of the ten species appearing at the base of this zone are restricted to it. These are *Globorotalia formosa formosa, G. formosa gracilis, Globigerina alanwoodi* El-Naggar and *G. turgida* Finlay. Nine species ranging up from the underlying zone occur here for the last time and eleven species range up into the overlying zone.

This zone was first recognized by Bolli (1957*a*) in Trinidad. It is regarded here as belonging to the lower part of the Lower Eocene.

5. The *Globorotalia aspensis*/*Globorotalia esnaensis* Zone

This is represented by samples 3140 to 3195 from the lower part of the Ghazij formation. It is characterized by the abundance of *Globorotalia aspensis* (Colom) and *G. esnaensis* (Le Roy). The lower limit is defined by the disappearance of *Globorotalia formosa formosa* Bolli, *G. formosa gracilis* Bolli, *G. marginodentata* Subbotina and *G. subbotinae* Morozova.

All eleven species occurring in this zone range up from the underlying zone, and none extends upwards into the higher zones. The stratigraphically significant species *Globorotalia aragonensis* Nuttall disappears in the lower part of the zone. The genus *Globigerina* is represented by two spinose species, *G. mckannai* White and *G. soldadoensis* Bronnimann. The two species of *Pseudohastigerina* which appear in the underlying zone become more common here.

This zone is tentatively correlated with the *Globorotalia aragonensis* Zone recognized by Bolli (1957*a*) in Trinidad, and is here assigned to the middle part of the Lower Eocene. It is followed directly by beds which contain only reworked Upper Cretaceous planktonic foraminifera.

6. The *Globorotalia crassata*/*Truncorotaloides topilensis* Zone

This is represented by the samples 3603 to 3609 from the upper Khirthar Formation. It is characterized by the presence of *Globorotalia crassata* (Cushman), *Truncorotaloides topilensis* (Cushman), *Globigerapsis kugleri* Bolli, Loblich & Tappan and *Globigerinoides higginsi* Bolli. Immediately underlying the strata representing this zone are beds with very rare, poorly preserved and indeterminable planktonic foraminifera. The upper limit of the zone is marked by the disappearance of *Truncorotaloides topilensis, Globigerapsis kugleri* and *Globigerinoides higginsi.*

None of the species occurring in the underlying zones are represented here. The representatives of seven genera, *Chiloguembelina, Hantkenina, Truncorotaloides, Globigerinita, Globigerinoides, Globigerapsis* and *Globigerinatheka* appear for the first time. With thirty-five species and subspecies representing ten genera, this zone contains the richest assemblage in the succession. Species of *Truncorotaloides,* and the spinose and keeled forms of *Globorotalia* dominate the fauna. Of the species occurring here, eleven are restricted to this zone while the remaining twenty-four range up in to the overlying zone. The genera *Hantkenina, Globigerapsis* and *Globigerinoides* are restricted to this zone, *Hantkenina* being represented by very rare specimens. *Globorotalia lehneri* Cushman & Jarvis is restricted to the lower part of the zone.

This zone is tentatively regarded as equivalent to the combined *Globorotalia lehneri* and *Orbulinoides beckmanni* (=*Porticulasphaera mexicana*) Zones recognized by Bolli (1957*c*) in Trinidad. It is assigned here to the middle part of the Middle Eocene.

7. The *Truncorotaloides rohri* Zone

This is represented by samples 3610 to 3647 from the upper Khirthar Formation. Samples 3627 to 3647 yielded rare and poorly preserved specimens and are only provisionally included in the zone which is characterized by the occurrence of *Truncorotaloides rohri* Bronnimann & Bermudez and *Globorotalia spinuloinflata* (Bandy) in abundance. In some samples from the upper part of the zone, representatives of *Chiloguembelina* and *Pseudohastigerina* are very abundant. In these samples, representatives of the other genera are rare. The upper limit of the zone is marked by the disappearance of *Truncorotaloides.*

Of the twenty-nine species and subspecies occurring here, twenty-four range up from the underlying zone. Among the five forms appearing for the first time, three, *Chiloguebelina goodwini* (Cushman & Jarvis), *C. woodi* sp. nov. and *G. baylissi* sp. nov. are restricted to it. Representatives of the genera *Truncorotaloides, Globorotalia* and *Globigerinatheka* do not range above this zone. Thirteen species and subspecies range up into the overlying zone. This zone correlates well with the *Truncorotaloides rohri* Zone in Trinidad (Bolli 1957*c*). It is assigned to the upper part of the Middle Eocene.

8. The *Globigerina officinalis* Zone

This is represented by samples 3650 to 3664 from the upper Khirthar Formation. The succeeding two samples 3665 and 3666 representing the topmost part of the succession did not yield planktonic foraminifera. It is characterized by the occurrence of *Globigerina officinalis* Subbotina, *G. augustiumbilicata* Bolli, *G. praebulloides leroyi* Blow & Banner and *G. praebulloides occlusa* Blow & Banner in considerable numbers.

Thirteen species and subspecies belonging to four genera, *Globigerina, Globigerinita, Pseudohastigerina* and *Chiloguembelina* occur in this zone. Of these, *Globigerina* is dominant, being represented by eight species and subspecies. The other three genera are poorly represented.

In the absence of more diagnostic foraminifera, direct correlation of this zone with those established for the late Eocene successions in well-known localities like Trinidad and Tanganyika is difficult. It seems to correspond to the interval represented by the *Globigerapsis mexicana* (=*Globigerapsis semiinvoluta*) and *Globorotalia cerroazulensis* Zones in Trinidad (Bolli 1957*c*), and is assigned here to the Upper Eocene.

SYSTEMATIC DESCRIPTIONS

The classification followed here is based on that of Bolli, Loeblich & Tappan (1957) with modifications and additions by later workers. It has been discussed in detail by the writer (1969, 1970*a*). Synonymies are restricted to the original description and to references providing important information on the taxonomy and distribution of the various species.

All figured specimens are deposited in the British Museum (Natural History).

Order FORAMINIFERIDA Eichwald 1830

Family **CHILOGUEMBELINIDAE** Reiss 1963

Genus ***CHILOGUEMBELINA*** Loeblich & Tappen 1956

TYPE SPECIES. *Guembelina midwayensis* Cushman 1940.

See Samanta (1969, 329) for discussion of genus.

Chiloguembelina goodwini (Cushman & Jarvis)

(Pl. 14, figs 7–8)

1933 *Gümbelina goodwini* Cushman & Jarvis (in Cushman): 69, pl. 7, figs 15a–16b.
1948 *Gümbelina goodwini* Cushman & Jarvis; Cushman & Renz: 23.

REMARKS. The number and the inflation of the chambers vary in the present material. The aperture is filled with crystalline material which often renders observation difficult. The chambers appear to be slightly more inflated than those in the holotype, but are otherwise closely comparable.

Drooger (1953), followed by Beckmann (1957), treated *C. goodwini* as a junior synonym of *C. martini* (Pijpers), but neither author gave his reasons. As indicated previously (Samanta 1969), the two species can be distinguished by their apertures.

In its symmetrical, high and narrow aperture, the specimen figured here closely resembles the holotype of *Chiloguembelina parallela* Beckmann, described from the *Globorotalia 'rex'* Zone of Trinidad.

DISTRIBUTION. *Chiloguembelina goodwini* was originally described from the Upper Eocene of Trinidad. Its range is reported to be Middle to Upper Eocene.

In the Rakhi Nala section it is restricted to the *Truncorotaloides rohri* Zone.

Chiloguembelina martini (Pijpers)

(Pl. 15, figs 13–14)

1933 *Textularia martini* Pijpers: 57, text-figs 6–10.
1953 *Gümbelina martini* (Pijpers); Drooger (pars): 100, pl. 1, fig. 2; non text-figs 4a–b.
1957 *Chiloguembelina martini* (Pijpers); Beckmann (pars): 89, pl. 21, figs 14a–b; text-fig 14 (9–11, 14–18, 20–23).
1968 *Chiloguembelina martini* (Pijpers); Raju: 291, pl. 1, fig. 12.

REMARKS. In the present material *C. martini* shows variation in the shape and size of the test, rate of enlargement and compression of the chambers, and the character of the aperture. Specimens with markedly twisted tests occur. The apertural flange is usually only partially preserved.

C. martini is readily distinguished from related species in the present material by its tendency to develop a twisted test and asymmetrical aperture, and by having less inflated chambers.

As indicated by the writer (1969), *Chiloguembelina goodwini* (Cushman & Jarvis) and *C. venezuelana* (Nuttall) are not junior synonyms of *C. martini*. These species can be distinguished by their apertural characters.

The specimen figured by Drooger (1953, text-figs 4a–b) as *Gumbelina martini* (Pijpers) differs from the types in having more inflated chambers and a semicircular aperture. It is morphologically very close to *C. venezuelana* (Nuttall).

DISTRIBUTION. *Chiloguembelina martini* was originally described from an Upper Eocene marl recovered from a well in Bonaire, Netherlands West Indies. Its stratigraphic range is reported as Lower to Upper Eocene. Raju (1968) recorded it from the Middle and Upper Eocene of southern India.

In the Rakhi Nala section, *C. martini* ranges from the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone to the base of the *Globigerina officinalis* Zone.

Chiloguembelina woodi sp. nov.

(Pl. 15, figs 15–16)

1970*b* *Chiloguembelina* sp. Samanta: 31, pl. b, figs 13, 14.

DIAGNOSIS. A *Chiloguembelina* with inflated, subglobular chambers between depressed, oblique sutures; surface smooth to weekly hispid; aperture large, semicircular to subcircular, bordered by a narrow lip-like structure.

DESCRIPTION. Test flaring, biserial; periphery lobate. Chambers arranged in 5 to 7 pairs, increasing regularly in size; those in the initial part of the test small and compressed, later becoming inflated, subglobular. Sutures oblique, slightly depressed in the early part becoming strongly depressed later. Surface almost smooth to weakly hispid. Aperture a large, semicircular to subcircular opening bordered by a narrow lip-like structure.

DIMENSIONS.

Holotype.	Length: 0·28 mm
Paratypes.	Length: 0·27 mm–0·33 mm

Locality and horizon. Types from sample No. 3622, Rakhi Nala section, West Pakistan.

Remarks. The chambers vary in number and in degree of inflation; the last two chambers also vary in size. The aperture varies in shape and size, and is often obscured by a crystalline infilling.

Among the Middle and Upper Eocene representatives of the genus, *C. venezuelana* (Nuttall) shows some resemblance to *C. woodi*. However, the latter can be distinguished by its more inflated chambers and larger aperture.

With its inflated subglobular chambers and large semi-circular aperture, *C. woodi* shows a relationship to *C. wilcoxensis* (Cushman & Ponton), a Palaeocene to Lower Eocene species from which it may have evolved.

The form from the Upper Eocene of the Mikir Hills, Assam, recorded by the writer (1970*b*) as *Chiloguembelina* sp., shares with *C. woodi* the inflated chambers, depressed sutures, and large subcircular aperture.

This species is named after Professor Alan Wood, Aberystwyth.

Distribution. In the Rakhi Nala section, *C. woodi* is restricted to the *Truncorotaloides rohri* Zone.

Family **GLOBIGERINIDAE** Carpenter, Parker & Jones 1862

Subfamily **GLOBIGERININAE** Carpenter, Parker & Jones 1862

Genus ***GLOBIGERINA*** d'Orbigny 1826

Type species. *Globigerina bulloides* d'Orbigny 1826.
See Samanta (1969) for discussion of genus.

Globigerina alanwoodi El-Naggar

(Pl. 3, figs 7–9)

1966 *Globigerina alanwoodi* El-Naggar: 156–157, pl. 16, figs 6a–c.

Remarks. When describing *Globigerina alanwoodi*, El-Naggar (1966) illustrated only the holotype and did not discuss variation. For its proper understanding, an examination was made of the holotype and 3 paratypes deposited in the British Museum (Natural History); the 3 paratypes in the Geology Department of the University College of Wales, Aberystwyth were also examined. The holotype is an ill-preserved, partially damaged specimen in which the aperture cannot be seen as the final chamber is incompletely preserved. The main variation observed in the 6 paratypes is in the shape of the spiral side of the test where the early chambers may be depressed below the outer whorl; in the number of chambers in the last whorl which usually enlarge somewhat irregular in size, and in the width of the umbilicus which is mostly filled with crystalline material obscuring the aperture. Around the umbilicus the surface of the chambers is distinctly papillose, while on the flattened spiral side of some paratypes the surface is finely pitted. The rest of the shell surface appears to be nearly smooth or very weakly papillose.

The Rakhi Nala specimens show all the distinctive features of *G. alanwoodi*. The surface of the test is distinctly papillose around the umbilicus and nearly smooth to faintly papillose elsewhere. The aperture in some specimens tends to extend partly outside the umbilicus. It appears to be furnished with a delicate lip. The dorsal side of the test is weakly convex to flat.

G. alanwoodi as noted by El-Naggar (1966 : 156), is closely related to *Globigerina mckannai* White, from which it differs in lacking the spinose surface ornamentation. El-Naggar suggested that *G. alanwoodi* might have evolved from *Globigerina spiralis* Bolli.

Distribution. *Globigerina alanwoodi* was first described from the lower part of the Upper Palaeocene of the Esna-Idfu region, Egypt.

In the Rakhi Nala section it occurs in the *Globorotalia formosa formosa* Zone.

Globigerina angustiumbilicata Bolli

(Pl. 1, figs 1–3)

1957*b* *Globigerina ciperoensis angustiumbilicata* Bolli: 109, pl. 22, figs 12a–13c.
1969 *Globigerina angustiumbilicata* Bolli; Samanta: 330, pl. 1, figs 1a–c.
1970*a* *Globigerina angustiumbilicata* Bolli; Samanta: 189, pl. 1, fig. 1.

Remarks. *G. angustiumbilicata* differs from *G. ciperoensis* Bolli in possessing a much smaller umbilicus and a lower and smaller aperture. The average size of the present specimens is less than that of *G. ciperoensis*, which usually has a higher dorsal spire and a coarser surface.

G. angustiumbilicata is very similar to *G. officinalis*, from which species it is believed to have been derived, but differs in that the rate of enlargement of the chambers is greater.

Distribution. According to reliable reports, this species ranges from the Middle Eocene to the Lower Miocene. It has been recorded from the Upper Eocene of eastern India (Samanta 1969) and from the Middle Eocene of western India (Samanta 1970*a*).

In the Rakhi Nala section *G. angustiumbilicata* ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Globigerina aquiensis Loeblich & Tappan

(Pl. 4, figs 1–3)

1957*a* *Globigerina aquiensis* Loeblich & Tappan: 180, pl. 51, figs 4a–5c; pl. 56, figs 4a–6c.
1970*c* *Globigerina aquiensis* Loeblich & Tappan; Samanta: 610, pl. 94, figs 1–2.

Remarks. The enlargement of the chambers in the last whorl is rather irregular. The final chamber often tends partly to cover the umbilicus The dorsal surface of the test seems to be smoother than the ventral one Owing to adherent matrix in the umbilical region, the apertural lip could not be observed clearly.

Distribution. The range of *G. aquiensis* is reported to be Upper Palaeocene to Lower Eocene. It has been reported by the writer (1970*c*) from the Upper Palaeocene, Pondicherry Formation of southern India.

In the Rakhi Nala section *G. aquiensis* ranges from the *Globorotalia velascoensis* Zone to the *Globorotalia formosa formosa* Zone.

Globigerina azerbaidjanica Khalilov
(Pl. 2, figs 1–3)

1956 *Globigerina azerbaidjanica* Khalilov: 243–244, pl. 4, figs 1a–c.

Description. Test inflated, coiled in a moderately high trochospire; dorsal side sub-conical; ventral side prominently convex; equatorial periphery roughly quadrangular, lobate; axial periphery rounded. Chambers on the dorsal side about 13, arranged in 3 whorls and enlarging very rapidly in size; chambers in the first whorl not very distinct; on the ventral side 3 large strongly inflated chambers very rapidly enlarging in size; the last chamber is perpendicular to the two preceding ones. Sutures on the dorsal side straight to slightly curved, moderately depressed; on the ventral side nearly straight, deeply depressed. Umbilicus well developed, deep and open. Surface of test finely pitted, hispid. Aperture interiomarginal, umbilical, a large semicircular opening bordered in some specimens by a weakly developed lip.

Remarks. *Globigerina azerbaidjanica* is characterized by a raised dorsal spire; 3 strongly inflated chambers in the last whorl, the final chamber situated across the two preceding ones and occupying about half of the whole ventral view of the test and a large umbilical aperture.

The Rakhi Nala specimens show variation in the height of the spire, the size of the final chamber and the size of the aperture. The initial chambers are too minute to be observed readily. There is an abrupt increase in the size of the chambers of the last whorl which occupies most of the test. The aperture is very often filled with crystalline material. The final chamber in some specimens appears to be smoother than the rest.

G. azerbaidjanica was compared by its author with *Globigerina posttriloculinoides* Khalilov, from which it was distinguished by its large semicircular umbilical aperture. In its rapidly enlarging, globular chambers in the last whorl and large umbilical aperture, *G. azerbaidjanica* shows some resemblance to *G. baylissi* sp. nov. However, the latter has more chambers in the last whorl, a more strongly lobate periphery and a radially elongate last chamber.

Distribution. *Globigerina azerbaidjanica* was originally described from the 'Lower upper Eocene' of the Maly Caucasus, Azerbaidzan, U.S.S.R.

In the Rakhi Nala section it ranges from the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone to the lower part of the *Globigerina officinalis* Zone.

Globigerina baylissi sp. nov.

(Pl. 2, figs 4–6)

DIAGNOSIS. A *Globigerina* with a roughly triglobular, elongate, hispid test coiled in a low trochospire; a strongly inflated, radially elongate final chamber constitutes about one-half of the test; the moderately large, arched umbilical aperture is furnished with a narrow lip.

DESCRIPTION. Test roughly triglobular, elongate, coiled in a low trochospire; ventral side more convex than the dorsal; equatorial periphery ovoid, elongate and strongly lobate; axial periphery rounded. Chambers inflated, globular and arranged in about three whorls; those in the initial whorl extremely small and tightly arranged; the last 3 chambers are large, strongly inflated and enlarge rapidly; the final chamber is radially elongate and constitutes about one half of the whole test; it often tends to be slightly displaced towards the ventral side. Sutures on the ventral side nearly straight, short and strongly depressed; on the dorsal side straight to slightly curved and moderately depressed. Umbilicus wide, open. Wall calcareous, finely perforate; surface weakly hispid. Aperture interio-marginal, umbilical, a moderately wide arched opening bordered with a narrow lip-like structure.

DIMENSIONS.

Holotype.	Maximum diameter: 0·31 mm
Paratypes.	Maximum diameter: 0·28 mm–0·30 mm

LOCALITY AND HORIZON. Types from sample No. 3622. Rakhi Nala section, West Pakistan.

REMARKS. The main variation is in the shape of the dorsal side of the test, the degree of lobation of the periphery, the shape and size of the final chamber and the character of the aperture. The initial chambers in some specimens are depressed below the outer whorl. The aperture varies in size and often tends to extend outside the umbilicus; in most specimens, including the holotype, it is filled with crystalline material. The final chamber may be larger than the rest of the test. In well preserved specimens the umbilicus tends to reveal the apertures of the earlier chambers in the last whorl.

G. baylissi is readily distinguished from contemporaneous species of the genus by its elongate test and large, strongly inflated and radially elongate last chamber. However, it resembles *Globigerina bulbosa* Le Roy (originally described from the Middle Miocene of Sumatra), which species has more prominently elongate, bulbous later chambers.

G. baylissi seems to have been derived from *G. inaequispira* by the development of the elongate test, more rapidly enlarging chambers in the last whorl and radially elongate final chamber, and transitional specimens were observed in the present material.

The species is named after Dr D. D. Bayliss whose samples formed the basis of the present investigation.

DISTRIBUTION. In the Rakhi Nala section *Globigerina baylissi* is restricted to the *Truncorotaloides rohri* Zone.

Globigerina ciperoensis Bolli

(Pl. 2, figs 10–12)

1945 *Globigerina cf. concinna* Reuss; Cushman & Stainforth: 67, pl. 13, figs 1a–b.
1954 *Globigerina ciperoensis* Bolli: 1–3, text-figs 3–4b.
1957*b* *Globigerina ciperoensis ciperoensis* Bolli; Bolli: 109, pl. 22, figs 10a–b.

Remarks. When reporting specimens from the Upper Eocene to Middle Oligocene of Ecuador, South America as *Globigerina* cf. *concinna* Reuss, Stainforth (1948 : 119) remarked that, 'This form has been variously described in tropical America as *G. concinna* and *G.* cf. *concinna* . . . It is probably a distinct species and because of its limited stratigraphic range deserves careful separation from the '*G. bulloides* tribe'.

Bolli (1954) proposed a new name, *Globigerina ciperoensis*, for this form and selected as holotype the specimen figured as *Globigerina* cf. *concinna* Reuss, by Cushman & Stainforth (1945) from the lower part of the Cipero formation of Trinidad. Later (1957*b*), he described two new subspecies, *G. ciperoensis angulisuturalis* and *G. ciperoensis angustiumbilicata*. He figured (Pl. 22, figs 10a–b) a paratype of *G. ciperoensis ciperoensis* showing its morphology in detail.

Blow & Banner (1962) examined topotype material from Trinidad and considered the three subspecies of *G. ciperoensis* described by Bolli as specifically distinct. They regarded *G. ciperoensis* as a subspecies of *G. ouachitaensis* Howe & Wallace.

The present specimens show all the diagnostic features of *G. ciperoensis* but also include individuals with higher dorsal spires than are seen in types and with more chambers in the last whorl. The height of the spire, rate of enlargement of the chambers in the last whorl and width of the umbilicus all show variations in this material. The specimen figured here compares well with the paratypes of *G. ciperoensis* illustrated by Bolli (1957*b*).

As indicated by Blow & Banner *G. ciperoensis* seems to have evolved from *G. ouachitaensis*, having acquired 5 chambers in the later whorls and a roughly pentagonal umbilicus.

Distribution. The holotype of *Globigerina ciperoensis* was originally described as *G.* cf. *concinna* Reuss from the Cipero formation of Trinidad. The stratigraphic range of *G. ciperoensis* is reported to be Upper Eocene to Lower Miocene.

In the Rakhi Nala section it ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the lower part of the *Globigerina officinalis* Zone.

Globigerina frontosa Subbotina

(Pl. 1, figs 22–24)

1953 *Globigerina frontosa* Subbotina: 84, pl. 12, figs 3–7.
1957*c* *Globigerina boweri* Bolli: 163, pl. 36, figs 1a–2b.

Remarks. The Rakhi Nala specimens closely resemble those from Trinidad described by Bolli (1957*c*) as *Globigerina boweri*, which species following Bermudez (1961) and Bandy (1964*b*) is here included in the synonymy of *G. frontosa* Subbotina.

Distribution. According to most authors this species ranges from Middle to Upper Eocene. The writer (1970*a*) has recorded it from the Middle Eocene of Western India.

In the Rakhi Nala section it ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the *Truncorotaloides rohri* Zone.

Globigerina haynesi El-Naggar

(Pl. 4, figs 7–9)

1966 *Globigerina haynesi* El-Naggar: 165–166, pl. 15, figs 5a–c.

Remarks. Variable features in the Rakhi Nala specimens are the convexity of the dorsal side of the test, the size of the final chamber and the width of the umbilicus. The specimen figured here resembles the holotype of *G. haynesi* in possessing a smaller final chamber that tends partly to cover the umbilicus.

The holotype and three paratypes deposited in the British Museum (Natural History) and the two paratypes deposited in the Geology Department, University College, Aberystwyth, were examined. The final chamber in the holotype is not perfectly preserved, and appears to be flattened on the ventral side. In contrast with the holotype, the paratypes include an individual having the final chamber larger than the penultimate one. The low, arched umbilical aperture is better seen in one of the paratypes than in the holotype.

The evolution of *G. haynesi* from *Globigerina spiralis* Bolli during the later part of the Lower Palaeocene (Danian) has been suggested by El-Naggar (1966 : 166, text-fig. 13).

Distribution. *Globigerina haynesi* was first described from the Esna-Idfu region of Egypt where it was observed to range from the uppermost part of the Danian to Upper Palaeocene.

In the Rakhi Nala section it occurs in the *Globorotalia velascoensis* Zone.

Globigerina inaequispira Subbotina

(Pl. 2, figs 7–9)

1953 *Globigerina inaequispira* Subbotina: 69, pl. 6, figs 1a–4c.

Remarks. The final chamber tends to be radially elongate and is very often slightly displaced towards the ventral side.

The present specimens agree well with the original description of *G. inaequispira*. The specimen figured here compares closely with the holotype, although the aperture in the former appears to be slightly higher. Individuals comparable to Subbotina's paratype (1953, figs 4a–c) and having radially elongate and peripherally widely separated later chambers, occur in the present material.

G. inaequispira is readily distinguished by its low trochospiral, strongly lobate and loosely coiled test with a tendency to develop radially elongate chambers. According to Berggren (1962 : 93) *G. inaequispira* has probably developed from *Globigerina pseudoeocaena* Subbotina in the Lower Eocene. *Globigerina foliata* Bolli, from the Miocene of Trinidad, closely resembles to *G. inaequispira*.

The specimens from North America described as *G. inaequispira* by Loeblich & Tappan (1957*a*) and by Olsson (1960) differ from Subbotina's form in having a tightly coiled test with a slightly lobate periphery. Again, the form illustrated by Hillebrandt (1962*b*, pl. 11, figs 12a–b) as *G. inaequispira* does not show clearly the characteristic features of the species.

The specimen figured by El-Naggar (1966, pl. 15, figs 8a–c) as *G. inaequispira* appears to be closely comparable to Subbotina's form. However, his specimens are from the Palaeocene while *G. inaequispira* appears only in the Lower Eocene elsewhere.

DISTRIBUTION. *Globigerina inaequispira* was originally described by Subbotina (1953) from her zone of conical Globorotalias, Northern Caucasus, U.S.S.R., which she dated as Lower to Middle Eocene.

In the Rakhi Nala section it ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the lower part of the *Globigerina officinalis* Zone.

Globigerina linaperta Finlay

1939*a* *Globigerina linaperta* Finlay: 125, pl. 13, figs 54–57.
1956 *Globigerina linaperta* Finlay; Haque: 173, pl. 8, figs 1a–c, 4a, b.

REMARKS. The main variation in the present specimens is in the rate of enlargement of the chambers in the last whorl, the degree of flattening of the later chambers and the character of the aperture.

DISTRIBUTION. The reported stratigraphic range of the species is Palaeocene to Upper Eocene. The writer (1969, 1970*a*, 1970*b*) recorded *G. linaperta* from the Middle and Upper Eocene of Assam, eastern India and from the Middle Eocene of Cutch, western India.

In the Rakhi Nala section *G. linaperta* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globigerina mckannai White

(Pl. 4, figs 13–15)

1928*a* *Globigerina mckannai* White: 194, pl. 27, figs 16a–c.

REMARKS. The convexity of the dorsal side of the test, the size and position of the final chamber and the width of the umbilicus all vary in the Rakhi Nala material. The surface of the test is weakly spinose. The umbilicus in most specimens is filled with extraneous material.

Globigerina dubia Egger var. *lakiensis* described by Haque (1956) from the Nammal limestone, Salt Range, West Pakistan, appears to be very close to *G. mckannai* White. Haque described it as having a cancellated surface. However, his figures seem to indicate the presence of fine spines on the surface of the holotype.

DISTRIBUTION. According to most workers *G. mckannai* ranges from the Upper Palaeocene to the Lower Eocene. Its occurrence in the Palaeocene Pondicherry formation of southern India has been observed by the writer (1970*c*).

In the Rakhi Nala section *G. mckannai* ranges from the *Globorotalia valascoensis* Zone to the *Globorotalia aspensis/Globorotalia esnaensis* Zone.

Globigerina nodosa El-Naggar

(Pl. 4, figs 4–6)

1966 *Globigerina nodosa* El-Naggar: 173–174, pl. 15, figs 6a–c.

Remarks. The Rakhi Nala specimens show variation in the inflation of the chambers, the size of the final chamber and in the intensity of surface ornamentation. In contrast to the holotype, the specimen figured here possesses fewer and more regularly enlarging chambers in the last whorl.

Distribution. *Globigerina nodosa* was first described from the Upper Palaeocene of Egypt. The writer (1970*c*) has observed well preserved specimens in the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. nodosa* occurs in the *Globorotalia aequa* and *Globorotalia formosa formosa* Zones.

Globigerina officinalis Subbotina

(Pl. 1, figs 7–9)

1953 *Globigerina officinalis* Subbotina (pars): 78, pl. 11, figs 1a–2c, 6a–7c, ?5a–c, non figs 3a–4c.

Distribution. *Globigerina officinalis* was first described from the Upper Eocene and Lower Oligocene of the Caucasus, U.S.S.R. It was later described (Bolli 1957*b*) as *Globigerina parva* from the Cipero formation of Trinidad. Its reported range is Middle Eocene to basal Miocene. It was recorded from the Middle and Upper Eocene of eastern India (Samanta 1969) and from the Middle Eocene of western India (Samanta 1970*a*).

In the Rakhi Nala section *G. officinalis* ranges from the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Globigerina ouachitaensis Howe & Wallace

(Pl. 1, figs 19–21)

1932 *Globigerina ouachitaensis* Howe & Wallace: 74, pl. 10, figs 7a–b.

Remarks. The Rakhi Nala specimens show variation in the height of the dorsal spire, lobation of the equatorial periphery and the size of the umbilicus. The final chamber varies from distinctly larger to slightly smaller than the penultimate one.

Distribution. *Globigerina ouachitaensis* was originally described in association with an Upper Eocene foraminiferal fauna. Its reported range is Middle Eocene to Lower Miocene.

In the Rakhi Nala section *G. ouachitaensis* ranges from the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Globigerina posttriloculinoides clinata Khalilov

(Pl. 1, figs 13–15)

1956 *Globigerina posttriloculinoides* Khalilov var. *clinata* Khalilov: 243, pl. 3, figs 3a–c.

Description. Test inflated, globular, coiled in a low trochospire; equatorial periphery roughly triangular, lobate; axial periphery rounded. Chambers inflated, globular forming 2½ to 3 rapidly enlarging whorls; initial chambers very small; the last whorl with 3 globular chambers which are much larger than those in the earlier whorls. Sutures straight to slightly curved, on the dorsal side moderately depressed and on the ventral side strongly depressed, incised. Umbilicus narrow, deep, open. Surface moderately pitted. Aperture an elongate slit-like opening with a narrow lip.

Remarks. In his original description, Khalilov mentioned that a distinctive feature was the deflection of the final chamber towards the ventral side of the test. However, this is not very clear in the holotype, with which the specimen figured here compares satisfactorily.

G. posttriloculinoides clinata appears to be related to the contemporaneous *G. linaperta-angiporoides* group.

Distribution. *Globigerina posttriloculinoides clinata* was originally described by Khalilov from the Upper Eocene of U.S.S.R.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globigerina praebulloides leroyi Blow & Banner

(Pl. 1, figs 4–6)

1953 *Globigerina officinalis* Subbotina (pars): 78, pl. 11, figs 4a–c, non figs 1a–3c, 5a–7c.
1958 *Globigerina globularis* Roemer; Batjes (pars): 161–162, pl. 11, figs 4a–c, non figs 3, 5.
1962 *Globigerina paraebulloides leroyi* Blow & Banner: 93, pl. 9, figs R–T; text-fig. 9 (v).

Remarks. Blow & Banner (1962) included in the synonymy of *G. praebulloides leroyi* a form from the Oligocene of Belgium identified by Batjes (1958) as *Globigerina globularis* Roemer. They considered *G. globularis* Roemer as *nomen dubium.* Recently, Butt (1966 : 86) identified late Oligocene specimens from Escornebeau as *G. globularis* which he regarded as a senior synonym of *G. praebulloides leroyi*. This synonymy is not accepted here.

The convexity of the dorsal side of the test, rate of enlargement of the chambers and the size of the final chamber vary in the present material.

With its 4 inflated chambers in the last whorl, lobate equatorial periphery and small umbilicus, *G. praebulloides leroyi* resembles *Globigerina officinalis* from which it is distinguished by its deeper umbilicus, symmetrical aperture and more coarsely perforate wall. Subbotina (1953 : pl. 11, fig. 4a–c) included a specimen of *G. praebulloides leroyi* as a paratype of *G. officinalis.*

According to Blow & Banner, *G. praebulloides leroyi* evolved from *G. praebulloides* *occlusa* by developing more inflated and embracing chambers, an almost closed umbilicus and a more laterally restricted aperture.

Distribution. *G. praebulloides leroyi* was first described from the Lindi area of Tanganyika where it was found to range from the Upper Eocene to the top of the Oligocene. Its total range is reported to be Upper Eocene to Lower Miocene.

In the Rakhi Nala section it ranges from the *Truncorotaloides rohri* Zone to the *Globigerina officinalis* Zone.

Globigerina praebulloides occlusa Blow & Banner

(Pl. 1, figs 16–18)

1962 *Globigerina praebulloides occlusa* Blow & Banner: 93–94, pl. 9, figs R–U; text-figs 14 (i–ii).
1969 *Globigerina praebulloides occlusa* Blow & Banner; Samanta: 331, pl. 1 figs 5a–c.
1970*a* *Globigerina praebulloides occlusa* Blow & Banner; Samanta: 191, pl. 1, figs 5–6.
1970*b* *Globigerina praebulloides occlusa* Blow & Banner; Samanta 33, pl. 6, figs 6–8.

Remarks. The main variation observed in the present material is in the degree of lobation of the periphery, size of the final chamber and in the character of the umbilicus. The initial whorl on the dorsal side of the test is slightly raised in some individuals. The sharp, minute spine bases between the fine pits give the surface a hispid appearance.

Earlier, workers had referred specimens of this subspecies to *Globigerina trilocularis* d'Orbigny, which according to Blow & Banner (1962 : 94) is a *nomen nudum.*

Much importance has been attached to this subspecies since its recognition as the ancestor of the stratigraphically significant *Globigerinoides* '*quadrilobatus*' group of forms (see Blow & Banner 1962 : 136–138).

Distribution. *G. praebulloides occlusa* was first described from the Oligocene of Tanganyika, East Africa. It was earlier reported by Bolli as *G.* cf. *trilocularis* d'Orbigny from Trinidad. The range of the subspecies is reported to be Middle Eocene to Lower Miocene. The writer (1969, 1970*b*) has recorded it from the Middle and Upper Eocene of eastern India and from the Middle Eocene of western India (Samanta 1970*a*).

In the Rakhi Nala section *G. praebulloides occlusa* ranges from the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Globigerina prolata Bolli

(Pl. 1, figs 10–12)

1957*a* *Globigerina prolata* Bolli: 72, pl. 15, figs 24–26.

Remarks. The surface of the test in well preserved specimens in my material is weakly hispid. The aperture is furnished with a narrow lip. The final chamber is usually deflected towards the ventral side as in the holotype.

Bolli (1957*a*) suggested that *G. prolata* was derived from *Globorotalia collactea* Finlay. However, Bolli's figured specimen (pl. 15, figs 21–23) of *G. collactea* from Trinidad differs distinctly from the holotype and the paratype of Finlay's species, which was well illustrated and redescribed by Jenkins (1965) who assigned it to *Truncorotaloides*.

The specimen from the Navet formation of Trinidad figured by Bolli (1957*c*, pl. 35, figs 7a–b) as *G. prolata* differs from the holotype in having a much smaller and centrally located aperture. Again, in the original description of *G. prolata*, Bolli mentioned that the surface of the test is smooth, while in the figures of the Navet specimen the surface of the test appears to be hispid.

Hillebrandt's (1962*b*) figured specimen of *Globigerina* cf. *prolata* differs from the Rakhi Nala specimens in having a flatter test, less inflated chambers and a lower aperture.

DISTRIBUTION. *G. prolata* was first described from the Lower Eocene, Upper Lizard Springs Formation of Trinidad where it ranges from the *Globorotalia formosa formosa* Zone to the *G. palmerae* Zone. In the Paderno d'Adda section of Northern Italy Bolli & Cita (1960*a*) reported it from the Lower Eocene *G. formosa formosa* Zone to the Middle Eocene, *Hantkenina aragonensis* Zone.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Globigerina soldadoensis Bronnimann

(Pl. 4, figs 10–12)

1952*b* *Globigerina soldadoensis* Bronnimann: 9–11, pl. 1, figs 1–9.
1970*c* *Globigerina soldadoensis* Bronnimann; Samanta: 612, pl. 95, figs 14, 15.

REMARKS. Bronnimann (1952*b*) stated that *G. soldadoensis* seemed to be related to the spinose *Globigerina decepta* Martin and to *Globigerina nitida* Martin, both described from the Lodo formation of California. This view was not accepted by later workers who considered *Globigerina mckannai* White to be the species from which *G. soldadoensis* had probably been derived.

DISTRIBUTION. *Globigerina soldadoensis* was originally described from the Palaeocene and Lower Eocene of Trinidad. The writer (1970*c*) has recorded it from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section it ranges from the upper part of the *Globorotalia velascoensis* Zone to the *Globorotalia aspensis/Globorotalia esnaensis* Zone.

Globigerina triangularis White

(Pl. 2, figs 13–15)

1928*a* *Globigerina triangularis* White: 195–196, pl. 28, figs 1a–b.
1957*a* *Globigerina triangularis* White; Bolli: 71, pl. 15, figs 12–14.
1965 *Globigerina triangularis* White; Proto Decima & Zorzi: 17, 18, pl. 1, figs 4a–c.

REMARKS. The original description and illustration of *G. triangularis* were not detailed enough for a thorough understanding of this species. Bolli (1957*a*) identified *G. triangularis* from the Palaeocene—Lower Eocene of Trinidad and illustrated one specimen well, showing the details of its morphology. The specimen figured here agrees well with that of Bolli. The apertural lip in my specimen is not preserved.

Loeblich & Tappan (1957*a* : 183) regarded *G. triangularis* as a junior synonym of *G. triloculinoides* Plummer, while Bolli (1957*c*) considered the former to have been derived directly from the latter. If *G. triangularis* is synonymised with *G. triloculinoides*, then the range of the latter will be Palaeocene to Lower Eocene.

DISTRIBUTION. *G. triangularis* was originally described from the lower part of the Velasco Formation, Mexico, where, according to Hay (1960), it ranges from the *Globorotalia uncinata* Subzone (Danian) to the *Globorotalia velascoensis* Zone (Upper Palaeocene). According to Bolli (1957*a*) the range of *G. triangularis* in Trinidad is Palaeocene, *G. pusilla pusilla* Zone to Lower Eocene, *G. aragonensis* Zone, Lizard Springs formation, possibly continuing into the overlying Navet formation.

In the Rakhi Nala section *G. triangularis* ranges from the *Globorotalia velascoensis* Zone to the *Globorotalia formosa formosa* Zone.

Globigerina triloculinoides Plummer

1926 *Globigerina triloculinoides* Plummer: 134–135, pl. 8, figs 10a–c.
1970*c* *Globigerina triloculinoides* Plummer; Samanta: 614, pl. 94, figs 5, 9, 13–16.

REMARKS. In her original description of *Globigerina triloculinoides* Plummer (1926) figured two specimens showing the dorsal and ventral views respectively. She designated the former as the type, and her description was adequate for a proper understanding of the species. Later, Loeblich & Tappan (1957*a* pl. 43, figs 9a–c) figured three views of a well-preserved topotype showing its morphology in detail.

A wide range of variation has been attributed to this species by some workers who have placed in synonymy forms which differ from the original description of *G. triloculinoides*. The writer does not follow Loeblich & Tappan (1957*a*) in regarding *Globigerina finlay* Bronnimann, *G. hornibrooki* Brönnimann, *G. stainforthi* Bronnimann and *G. triangularis* White as synonyms of *G. triloculinoides*.

Individuals closely comparable to *G. pseudotriloba* White occur in the Rakhi Nala material. They are not treated here separately. White's species shows all the distinctive features of *Globigerina incisa* Hillebrandt, described from the Palaeocene of Austria. When describing *G. incisa*, Hillebrandt (1962*b*) did not compare it with *G. pseudotriloba*.

G. triloculinoides is believed to have evolved from *Globorotalia pseudobulloides* (Plummer) by a reduction in the number of chambers in the last whorl, the development of coarsely reticulate surface ornamentation and the confinement of the aperture to an intraumbilical-umbilical position.

DISTRIBUTION. According to most workers the range of *G. triloculinoides* is Lower Palaeocene (Middle Danian) to Upper Palaeocene. It is well represented in the Palaeocene Pondicherry formation of southern India (Samanta 1970*c*).

In the Rakhi Nala section *G. triloculinoides* ranges from the *Globorotalia angulata* Zone to the *Globorotalia aequa* Zone.

Globigerina turgida Finlay

(Pl. 3, figs 4–6)

1939*a* *Globigerina linaperta* Finlay var. *turgida* Finlay: 125.
1952*b* *Globigerina turgida* Finlay; Bronnimann: 19–21, pl. 3, figs 1–3.
1964 *Globorotaloides turgida* (Finlay); Jenkins: 117–118, pl. 7, figs 1a–11a, 1b–10b; pl. 8, figs 1c–11c, 1d–10d, 11–12, 13a–c.

Remarks. *G. turgida*, when originally erected as a variety of *Globigerina linaperta* was neither figured nor adequately described. Bronnimann (1952*b*), examined topotypes of *G. turgida* and of *G. linaperta* and considered them to be separate species.

Jenkins (1964) figured the holotype of *G. turgida* showing its morphology in detail for the first time. He discussed its ontogeny on the basis of specimens from the type sample, and considered it to belong to the genus *Globorotaloides* Bolli.

Bolli's (1957*a*, pl. 15, figs 3–5) figured specimen of *G. turgida* from the Lower Eocene, *Globorotalia aragonensis* Zone, Upper Lizard Springs formation of Trinidad lacks the characteristic umbilical bulla, while his figured specimen from the *G. palmerae* Zone (on. cit. pl. 35, figs 13a–c), Navet formation with a high trochospirally coiled test seems to be specifically distinct from Finlay's form.

The specimen from the Middle Eocene of Puerto Rico figured by Pessagno (1961, pl. 2, figs 3–5) differs from the holotype in having a low conical test and in lacking the umbilical bulla.

Distribution. *G. turgida* was originally described from the Middle Eocene of New Zealand. Jenkins (1964) gave its range as Eocene, but later (1966*a*) extended it into the Palaeocene.

In the Rakhi Nala section it occurs in the *Globorotalia formosa formosa* Zone.

Globigerina velascoensis Cushman

(Pl. 3, figs 10–12)

1925*b* *Globigerina velascoensis* Cushman: 19, pl. 3, figs 6a–c.
1970*c* *Globigerina velascoensis* Cushman; Samanta: 615, pl. 94, figs 7, 8.

Remarks. In the present material *G. velascoensis* shows appreciable variation in the degree of peripheral flattening of the later chambers and in the size of the final chamber.

According to Bolli (1957*a* : 71) *G. velascoensis* was apparently developed from *G. triangularis* White.

Distribution. *Globigerina velascoensis* was originally described from the Velasco formation of Mexico, where Hay (1960) found it to range from the *Globorotalia uncinata* Subzone (Upper Danian), to the top of the *Globorotalia velascoensis* Zone (Upper Palaeocene). Typical representatives of the species were found by the writer (1970*c*) in the Palaeocene Pondicherry Formation of southern India.

In the Rakhi Nala section *G. velascoensis* is restricted to the *Globorotalia velascoensis* Zone.

Globigerina yeguaensis Weinzierl & Applin

(Pl. 3, figs 1–3)

1929 *Globigerina yeguaensis* Weinzierl & Applin: 408, pl. 43, figs 1a–b.

Remarks. *G. yeguaensis* is the largest species of this genus in the present material. The figured specimen closely resembles the holotype.

There is considerable difference of opinion about the true range of variation of this species. Weinzierl & Applin (1929) illustrated only the holotype and showed its dorsal and ventral sides. They did not describe any variation seen in their material.

Bolli (1957*c* : 163), in discussing material from the Middle to Upper Eocene of Trinidad, remarked that 'There is considerable variation in the specimens regarded as belonging to *Globigerina yeguaensis*'. He figured two specimens to show the main variation. One (pl. 35, fig. 15a–c), was later included by Bermudez (1961 : 1183) in the synonymy of his new species *Globigerina galavisi*.

Berggren (1960*a*) lumped together several species under *G. yeguaensis*. The statistical analysis of three assemblages from the Lower Eocene of Denmark and northwestern Germany (Berggren & Kurten 1961) indicated that this species is highly variable.

Distribution. The reported range of *G. yeguaensis* is Lower Eocene to Oligocene. It has been recorded by the writer from the Middle and Upper Eocene of eastern India (Samanta 1969, 1970*b*) and from the Middle Eocene of western India (Samanta 1970*a*.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Genus ***GLOBIGERINITA*** Bronnimann 1951, emended Blow & Banner 1962

Type species. *Globigerinita naparimaensis* Bronnimann 1951.

Globigerinita africana Blow & Banner

(Pl. 5, figs 7–9)

1962 *Globigerinita africana* Blow & Banner: 105–106, pl. 15, figs A–C; text-fig. 11, (i–iv).

Remarks. The specimen figured here resembles the paratype of *G. africana* Blow & Banner (text-fig. 11 (iv)) in possessing four accessory openings in the umbilical bulla. The Rakhi Nala material shows less variation than that reported by Blow & Banner (1962).

Distribution. The reported range of *G. africana* is Middle-Upper Eocene. The writer (1970*a*) has reported it from the Middle Eocene *Orbulinoides beckmanni* Zone in Western India.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globigerinita dissimilis (Cushman & Bermudez)

(Pl. 5, figs 10–12)

1937 *Globigerina dissimilis* Cushman & Bermudez: 25–26, pl. 3, figs 4–6.
1961 *Globigerinita dissimilis* (Cushman & Bermudez); Bermudez: 1262–1263, pl. 7, figs 4–5.
1970*b* *Globigerinita dissimilis* (Cushman & Bermudez); Samanta: 35, pl. 6, fig. 1.

REMARKS. Cushman & Bermudez (1937) illustrated three specimens, the holotype and two paratypes, showing the ventral, peripheral, and dorsal views respectively. Later, Bolli, Loeblich & Tappan (1957 : 36) designated it as the type species of their new genus *Catapsydrax* and gave three views of the holotype showing its morphology in detail. They also figured two specimens from the Cipero formation of Trinidad to demonstrate the main morphological variation. Subsequently, *Catapsydrax* was regarded as synonymous with *Globigerinita* Bronnimann by Bermudez (1961) and Blow & Banner (1962).

The surface of the test is weakly hispid in the present specimens. The accessory openings are bordered by weakly developed narrow lip-like structures. In some specimens they are filled with extraneous material which renders satisfactory observation difficult.

DISTRIBUTION. The range of *G. dissimilis* is reported to be from the upper part of the Middle Eocene to the Lower Miocene. Samanta (1970*b*) has recorded it from the Upper Eocene of the Mikir Hills, Assam.

In the Rakhi Nala section it ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Globigerinita echinata (Bolli)

(Pl. 5, figs 4–6)

1957*c* *Catapsydrax echinatus* Bolli: 165–166, pl. 37, figs 2a–5b.
1961 *Globigerinita echinata* (Bolli); Burmedez: 1263–1264.

REMARKS. The convexity of the dorsal side of the test, lobation of the equatorial periphery, intensity of the surface ornamentation and the character of the bulla vary in the present material. The surface of the bulla is usually smoother than that of the rest of the test. The accessory openings are furnished with a very narrow smooth border.

G. echinata is a distinctive form of the genus. It is readily distinguished from contemporaneous species by its characteristic spinose surface.

DISTRIBUTION. *Globigerinita echinata* was originally described from Trinidad where it was observed to range from the upper part of the *Globorotalia lehneri* Zone to the lower part of the *Truncorotaloides rohri* Zone.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Globigerinita howei Blow & Banner

(Pl. 5, figs 13–15)

1962 *Globigerinita howei* Blow & Banner: 109–110, pl. 14, figs P–R; text-fig. 11 (x–xiv).
1969 *Globigerinita howei* Blow & Banner; Samanta: 332, pl. 1, figs 3a–c.

Remarks. *G. howei* is easily distinguished from other species of the genus in the Rakhi Nala section by its exceptionally inflated, large bulla.

Distribution. *Globigerinita howei* was first described from Tanganyika, East Africa. Its reported range is Middle-Upper Eocene. This species has been recorded by the writer (1969) from the Upper Eocene of Assam, eastern India.

In the Rakhi Nala section *G. howei* ranges from the *Globorotalia crassata/Truncorotaloides topilensia* Zone to the *Globigerina officinalis* Zone.

Genus ***GLOBIGERINOIDES*** Cushman 1927

Type species. *Globigerina rubra* d'Orbigny 1839.

Globigerinoides higginsi Bolli

(Pl. 5, figs 1–3)

1957*c* *'Globigerinoides' higginsi* Bolli: 164–165, pl. 36, figs 11a–13b.
1968 *Globigerinoides higginsi* Bolli; Raju: 290, pl. 2, figs 7a–b.
1970*a* *Globigerinoides higginsi* Bolli; Samanta: 194, pl. 2, fig. 15.

Remarks. The surface of the test in well-preserved specimens is weakly hispid. The chambers enlarge regularly in size. Usually one dorsal sutural aperture is present at the intersection of the spiral suture with the intercameral suture between the penultimate and final chambers. It is often too minute to be observed clearly.

Distribution. The reported range of *G. higginsi* is from the upper part of Lower Eocene to the Middle Eocene. It has been reported from southern and western India (Raju 1968; Samanta 1970*a*).

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Subfamily **ORBULININAE** Schultze 1854

Genus ***GLOBIGERAPSIS*** Bolli, Loeblich & Tappan 1957

Type species. *Globigerapsis kugleri* Bolli, Loeblich & Tappan 1957.

1962 *Globigerapsis* Bolli, Loeblich & Tappan; Blow & Banner: 123–124 (see for discussion).

Globigerapsis kugleri Bolli, Loeblich & Tappan

(Pl. 6, figs 4–6)

1957 *Globigerapsis kugleri* Bolli, Loeblich & Tappan: 34, pl. 6, figs 6a–c.
1968 *Globigerapsis kugleri* Bolli, Loeblich & Tappan; Raju: 290, Pl. 2, figs 8a–b.
1970*a* *Globigerapsis kugleri* Bolli, Loeblich & Tappan; Samanta: 198, pl. 2, figs 11–13.

Remarks. The size of the last chamber, the degree of depression of the sutures and the number of sutural openings vary in this material. The final chamber may constitute about one half of the test. The apertural openings are bordered by distinct, narrow rims. The specimen figured here compares well with the holotype.

Distribution. According to Bolli (1957*c*) this species ranges from the upper part of the *Globigerapsis kugleri* Zone to the top of the *Orbulinoides beckmanni* Zone in Trinidad. It has also been reported from Barbados, Cuba, France, western and southern India (Samanta 1970*a*; Raju 1968).

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Globigerapsis tropicalis Blow & Banner

(Pl. 6, figs 7–8)

1962 *Globigerapsis tropicalis* Blow & Banner: 124–125, pl. 15, figs D–F.
1970*a* *Globigerapsis tropicalis* Blow & Banner; Samanta: 199, pl. 2, fig. 18.
1970*b* *Globigerapsis tropicalis* Blow & Banner; Samanta: 35, pl. 6, figs 21–23.

Distribution. The reported range of *G. tropicalis* is Middle-Upper Eocene. The writer (1970*a* and *b*) has recorded it from the Middle Eocene of western India and from the Upper Eocene of eastern India. Raju (1968) has figured a specimen comparable to *G. tropicalis* from the Middle Eocene of southern India.

In the Rakhi Nala section *G. tropicalis* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Genus ***GLOBIGERINATHEKA*** Bronnimann 1952

Type species. *Globigerinatheka barri* Bronnimann 1952.

Globigerinatheka barri Bronniman

(Pl. 6, figs 1–3)

1952*a* *Globigerinatheka barri* Bronnimann (pars): 27–28, text-figs 3a–c, g–h, *non* text-figs 3d–f.
1968 *Globigerinatheka barri* Bronnimann; Raju: 290–291, pl. 2, fig. 6.

Remarks. The size of the final chamber, the number and size of the sutural bullae and the number of accessory openings vary in the material. The maximum number of bullae observed is four. Each bulla is usually provided with 2 to 3 accessory openings which are bordered by distinct narrow rims. It is the only representative of the genus observed in the Rakhi Nala material.

Distribution. This characteristic species has been reported from a number of areas including western and southern India. Its reported range is Middle to Upper Eocene.

In the Rakhi Nala section *G. barri* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Family **GLOBOROTALIIDAE** Cushman 1927

Genus ***GLOBOROTALIA*** Cushman 1927

TYPE SPECIES. *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady 1877.

1965 *Globorotalia* Cushman; Luterbacher: 635–646 (see for discussions).

Globorotalia acuta Toulmin
(Pl. 10, figs 8–10)

1941 *Globorotalia wilcoxensis* Cushman & Ponton var. *acuta* Toulmin: 608, pl. 82, figs 6–8.
1970*c* *Globorotalia acuta* Toulmin; Samanta: 615, pl. 97, figs 1, 2.

DISTRIBUTION. According to most authors *G. acuta* is restricted to the Upper Palaeocene. Samanta (1970*c*) has examined well-preserved typical representatives of *G. acuta* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section it occurs in the *Globorotalia velascoensis* and *Globorotalia aequa* Zones.

Globorotalia aequa Cushman & Renz
(Pl. 10, figs 1–4)

1942 *Globorotalia crassata* (Cushman) var. *aequa* Cushman & Renz: 12, pl. 3, figs 3a–c.

REMARKS. The main variation in the Rakhi Nala specimens is in the shape of the dorsal side of the test, the size of the final chamber and the intensity of the surface ornamentation, specifically along the periphery. Specimens with weakly developed spinose peripheral keels were observed.

DISTRIBUTION. According to most authors this species ranges from the base of the Upper Palaeocene to the Lower Eocene. Well preserved, abundant specimens of *G. aequa* were examined by the writer (1970*c*) from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section it ranges from the *Globorotalia angulata* Zone to the *Globorotalia formosa formosa* Zone.

Globorotalia angulata (White)
(Pl. 8, figs 7–9)

1928 *Globigerina angulata* White: 191–192, pl. 27, figs 13a–c.
1970*c* *Globorotalia angulata* (White); Samanta: 619, pl. 96, figs 6–8.

REMARKS. The main variation in the present specimens is in the number and rate of enlargement of the chambers in the last whorl, the character of the final chamber and the ornamentation along the periphery of the test. The final chamber may be smaller than the penultimate chamber. A faint, spinose peripheral keel is observed in some individuals.

DISTRIBUTION. *G. angulata* was originally described from the Velasco formation of Mexico where, according to Hay (1960), it ranges from the upper part of the *Globorotalia uncinata* Subzone to the top of the *Globorotalia velascoensia* Zone.

Well preserved, abundant material of *G. angulata* from the Palaeocene Pondicherry Formation of southern India were examined by the writer (1970*c*).

In the Rakhi Nala section it ranges from the *Globorotalia angulata* Zone to the *Globorotalia velascoensis* Zone.

Globorotalia aragonensis Nuttall

(Pl. 8, figs 4–6)

1930 *Globorotalia aragonensis* Nuttall: 288–289, pl. 24, figs 6–8, 10–11.
1937*a* *Globorotalia aragonensis* Nuttall; Glaessner: 30, pl. 1, figs 5a–c.
1956 *Globorotalia aragonensis* Nuttall; Haque: 180, pl. 4, figs 4a–c.
1957*a* *Globorotalia aragonensis* Nuttall; Bolli: 75, pl. 18, figs 7–9.
1961 *Pseudogloborotalia aragonensis* (Nuttall); Bermudez: 1338–1340, pl. 16, figs 5a–c.
1965 *Globorotalia aragonensis* Nuttall; Luterbacher: 696, figs 121–123 only.
1968 *Globorotalia aragonensis* Nuttall; Raju: 288, pl. 3, figs 6a–c.

REMARKS. The main variation observed in the Rakhi Nala material is in the number and rate of enlargement of the chambers in the last whorl, the size of the umbilicus and the peripheral ornamentation. The dorsal side in most specimens is flattened. The umbilical ends of the chambers are tightly arranged. The chambers in the last whorl do not always enlarge regularly.

When describing *G. aragonensis*, Nuttall (1930) figured the dorsal, ventral and peripheral views of one specimen and the dorsal and ventral views respectively of two others. He did not designate a holotype. Nuttall mentioned the close morphological resemblance of his form to *G. velascoensis* (Cushman) from which he distinguished it by its smaller umbilicus, fewer chambers in the last whorl and more elevated dorsal surface.

Bolli (1957*a*) considered that *G. aragonensis* was not directly related to *G. velascoensis*. In the Rakhi Nala material, this species is easily distinguished from *G. velascoensis* by its smaller test, more tightly arranged chambers in the last whorl, much smaller umbilicus, unornamented and tightly arranged umbilical chamber tips and weaker peripheral keel. According to Luterbacher (1965 : 696) the sutures on the dorsal side 'form a distinct and characteristic angle with the periphery'.

The specimen from Trinidad figured by Cushman & Renz (1948, pl. 8, figs 1–2) as *Globorotalia aragonensis* differs specifically from Nuttall's form in having an almost equally biconvex test and in lacking a peripheral keel.

Haque's (1956, pl. 4, figs 4a–c) figured specimen from the basal Laki of the Nammal Gorge, West Pakistan shows a somewhat lower test and smoother surface. Otherwise it agrees with the original definition of *G. aragonensis*.

Of the six specimens figured by Luterbacher (1965) from the Gubbio section of Central Italy, one (figs 126a–c) with 4 very rapidly enlarging chambers in the last whorl seems to be specifically distinct.

Globorotalia caucasica Glaessner, originally described as a variety of *G. aragonensis*, differs from Nuttall's species in having a much wider umbilicus, steeper lateral sides of the chambers in the last whorl, ornamented umbilical shoulders and a more prominent peripheral keel.

Mallory (1959) described a new variety, *G. aragonensis* Nuttall var. *twisselmanni*, from the Lower Eocene of California, which he distinguished from *G. aragonensis* by its more strongly curved dorsal sutures, fewer chambers in the last whorl and usually larger umbilicus. An examination of the type material of Mallory's form is necessary to determine its true relationship to *G. aragonensis*.

Distribution. *G. aragonensis* was originally described by Nuttall from the Aragon Formation of the Tampico region of Mexico. He assigned a Lower Eocene age to the Aragon Formation. However, according to Luterbacher (1965 : 696) 'the occurrence of *Hantkenina aragonensis* in its type-sample indicates a Middle Eocene age'. According to Bolli (1957*a*, *c*), it ranges from the Lower Eocene, *G. formosa formosa* Zone to the Middle Eocene, *Globigerapsis kugleri* Zone in Trinidad. Haque (1956) has reported *G. aragonensis* from the Laki of the Nammal gorge, West Pakistan. It was recently reported by Raju (1968) from the subcrops of the Cauvery basin where he found it to range from the Lower Eocene to the lower part of the Middle Eocene.

In the Rakhi Nala section *G. aragonensis* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis*/*Globorotalia esnaensis* Zones.

Globorotalia aspensis (Colom)

(Pl. 15, figs 10–12)

1954 *Globigerina aspensis* Colom: 151–152, pl. 3, figs 1–35, pl. 4, figs 1–31.
1957*c* *Globorotalia aspensis* (Colom); Bolli: 166–167, pl. 37, figs 18a–c.
1961 *Globigerina aspensis* Colom; Bermudez: 1157–1158, pl. 1, figs 2a–c.
1965 *Acarinina aspensis* (Colom); Hillebrandt: 20.

Remarks. In the original description of *G. aspensis*, Colom (1954) figured numerous specimens which he regarded as belonging to two different groups, 'formas aplanadas' and 'formas trocoidales' respectively. He did not designate a holotype. It seems that only one view of each specimen was figured. His figures were of rather low magnification and the details of some morphological features are not clearly discernable.

When reporting this species from Trinidad, Bolli (1957*c*, 167) remarked that 'The position of the apertures in the type specimens of *Globigerina aspensis* figured by Colom is interiomarginal, umbilical-extraumbilical. For this reason the species is here placed in *Globorotalia*'. He also mentioned that in material from the lower Navet formation of Trinidad, *G. aspensis* shows a range of variation similar to that reported by Colom in his original description. Bolli's (1957*c*, pl. 37, figs 18a–c) figured specimen of *G. aspensis* shows more chambers in the last whorl than that reported by Colom.

Bermudez (1961 : 1157–1158, 1167) postulated that the two groups of forms distinguished by Colom (1954) belong to two different species. Accordingly he proposed the new species *Globigerina colomi* Bermudez for the specimens included by Colom in 'formas trocoidales'. It may be possible that more than one species was included in Colom's original concept of *G. aspensis*. However, an examination of Colom's figures alone without a re-examination of his figured material, does not permit a definite decision on this matter.

According to Bolli (1957*c*) *G. aspensis* has probably developed from *Globigerina soldadoensis* Bronnimann.

DISTRIBUTION. *G. aspensis* was originally described from Alicante, south-eastern Spain, where it was found to range from the Upper Ypresian to the Lower Lutetian. Bolli (1957*c*) reported it from the *Globorotalia palmerae* Zone to the *Globigerapsis kugleri* Zone in Trinidad. The reported range of *G. aspensis* is from Lower Eocene to the lower part of the Middle Eocene.

In the Rakhi Nala section *G. aspensis* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis*/*Globorotalia esnaensis* Zones.

Globorotalia broedermanni Cushman & Bermudez

(Pl. 15, figs 4–6)

1949 *Globorotalia* (*Truncorotalia*) *broedermanni* Cushman & Bermudez: 40, pl. 7, figs 22–24.

1957*a* *Globorotalia broedermanni* Cushman & Bermudez; Bolli: 80, pl. 19, figs 13–15.

1961 *Pseudogloborotalia broedermanni* (Cushman & Bermudez); Bermudez: 1340, pl. 16, figs 6a–c.

1968 *Globorotalia broedermanni* Cushman & Bermudez; Raju: 288, pl. 3, figs 3a–c.

REMARKS. The shape of the test in peripheral view and the intensity of the surface ornamentation vary in the present material. The enlargement of the chambers in the last whorl is often irregular. The specimen figured here possesses more chambers in the last whorl than does the holotype.

Cushman & Bermudez (1949) figured the dorsal view of the holotype and ventral and peripheral views of the paratype. They compared *G. broedermanni* with the Palaeocene species *G. albeari* Cushman & Bermudez, from which it was distinguished by its more open umbilicus and less acute periphery. According to the original description the number of chambers in the last whorl is greater in *G. albeari* than in *G. broedermanni*. The two species seem to be directly related.

Bolli's (1957*c*, pl. 37, figs 13a–c) figured specimens from the *Globorotalia palmerae* Zone, Navet formation of Trinidad differs somewhat from the original description of *G. brodermanni* in showing more, and less tightly arranged, chambers in the last whorl, a more lobate periphery and slightly more inflated later chambers. It also differs from the specimen figured by the same author (1957*a* pl. 19, figs 13–15) from the *Globorotalia formosa formosa* Zone, upper Lizard Springs formation of Trinidad.

Gohrbandt (1967*b* : 322) remarked that his Middle Eocene specimens of *Globorotalia mattseensis* from Austria 'are very close to *Globorotalia broedermanni* as illustrated by Bolli (1957*b*, pl. 37) from Trinidad, from the *Globorotalia palmerae* Zone, uppermost Lower Eocene . . . It is possible that the forms determined by Bolli as *Globorotalia broedermanni* in the *Hantkenina aragonensis* and *Globigerapsis kugleri* Zones of Trinidad are actually the morphologically similar *Globorotalia mattseensis* . . . The form illustrated by Bolli from the *Globorotalia palmerae* Zone of Trinidad might be transitional between *Globorotalia broedermanni* and *Globorotalia mattseensis*'. It may be possible that Gohrbandt's species is closely related to *G. broedermanni*.

However, the figured paratype of *G. mattseensis*, considered by Gohrbandt as an immature individual, seems to show a closer resemblance to *Globorotalia aspensis* (Colom).

DISTRIBUTION. *Globorotalia broedermanni* was originally described from the Lower Eocene of Cuba. It was thought to be a good index fossil for the Capdevila Formation. Bolli (1957*a*, *c*) reported it from Trinidad where he gave its range as *Globorotalia 'rex'* Zone to *Globigerapsis kugleri* Zone. Raju (1968) has reported *G. broedermanni* from the Cauvery Basin, southern India where he found it to range from the Lower Eocene to the lower Middle Eocene.

In the Rakhi Nala section, *G. broedermanni* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis/Globorotalia esnaensis* Zones.

Globorotalia centralis Cushman & Bermudez

(Pl. 12, figs 10–12)

1937 *Globorotalia centralis* Cushman & Bermudez: 26–27, pl. 2, figs 62–65.
1968 *Turborotalia centralis* (Cushman & Bermudez); Raju: 290–291, pl. 4, figs 3a–c.
1969 *Globorotalia centralis* Cushman & Bermudez; Samanta: 333, pl. 2, figs 2a–c.
1970*a* *Globorotalia centralis* Cushman & Bermudez; Samanta: 203, pl. 1, figs 18–20.
1970*b* *Globorotalia centralis* Cushman & Bermudez; Samanta: 36.

REMARKS. In describing this species, Cushman & Bermudez showed a peripheral view of the holotype, and ventral, peripheral and dorsal views respectively of three paratypes. They did not adequately enlarge their figures. Bolli, Loeblich & Tappan (1957) provided three good illustrations of the holotype.

G. centralis is easily distinguished from the contemporaneous species of the genus in the Rakhi Nala material by its inflated chambers, nearly smooth surface, rounded periphery of the test, and large open aperture.

DISTRIBUTION. This species has been recorded from the Middle and Upper Eocene of southern India (Raju 1968), from the Middle and Upper Eocene of eastern India (Samanta 1969, 1970*b*) and from the Middle Eocene of western India (Samanta 1970*a*).

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globorotalia chapmani Parr

(Pl. 13, figs 13–15)

1938 *Globorotalia chapmani* Parr: 87, pl. 3, figs 8–9b.
1970*c* *Globorotalia chapmani* Parr; Samanta: 621, pl. 98, figs 15–18.

REMARKS. Parr (1938) described *Globorotalia chapmani* from borings in the Perth Basin, Western Australia. He figured the ventral and the peripheral views of the holotype and the dorsal view of another specimen. However, his figures were not sufficiently detailed. He regarded *G. chapmani* as an Upper Eocene species.

McGowran (1964), after a re-examination of Parr's original material, concluded that the King's Park Shale, from which *G. chapmani* was described, is Palaeocene in age. He illustrated four specimens, including Parr's paratype, showing the distinctive features of *G. chapmani*. However, he neither re-illustrated the holotype nor commented on its morphology. Again, only the dorsal view of the paratype was shown.

The concept of *G. chapmani* followed here is based on McGowran's discussion and illustration.

In the present material, the rate of enlargement of the chambers in the last whorl, the degree of lobation of the periphery, and the angularity of the axial periphery all display variation. The inner whorls on the dorsal side may be raised in some specimens. From stereoscan illustrations (see Samanta 1970*c*) it appears that the peripheral margin of *G. chapmani* may not be wholly imperforate. The pores in the periphery, when present, are much finer and more widely spaced than those in the other parts of the surface.

G. chapmani is closely related to *Globorotalia compressa* (Plummer) from which it differs in having more compressed chambers and in the character of the periphery of the test. It has been suggested that it was derived from Plummer's form. Berggren & Olsson (1967) have attributed much significance to *G. chapmani* by considering it as the direct ancestor of the planispiral genus *Pseudohastigerina* Banner & Blow.

DISTRIBUTION. *G. chapmani* has been reported to range from the Middle to Upper Palaeocene. The writer (1970*c*) has observed typical representatives in the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section it occurs in the *Globorotalia velascoensis* Zone.

Globorotalia conicotruncata Subbotina

(Pl. 8, figs 1–3)

1947 *Globorotalia conicotruncata* Subbotina: 115–117, pl. 4, figs 11–13, pl. 9, figs 9–11.
1953 *Acarinina conicotruncata* (Subbotina); Subbotina: 220, pl. 20, figs 5a–8c, 10a–c; *non.* figs 9a–c, 11a–12c.

REMARKS. Unlike Subbotina (1947, 1953), the writer restricts his concept of this species to specimens with more than 5 chambers in the last whorl. The present specimens show all the distinctive features of the types of *G. conicotruncata*.

DISTRIBUTION. According to reliable reports the species ranges from the base of the Middle Palaeocene to the Upper Palaeocene. The writer has examined well-preserved specimens of *G. conicotruncata* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. conicotruncata* ranges from the *Globorotalia angulata* Zone to the *Globorotalia velascoensis* Zone.

Globorotalia crassata (Cushman)

(Pl. 11, figs 7–9)

1925*d* *Pulvinulina crassata* Cushman: 300–301, pl. 7, fig. 4.
1964*a* *Globorotalia crassata* (Cushman); Bandy: 34–35, text-fig. 1a–c.

REMARKS. The specimen figured here agrees well with the description and illustrations of the lectotype of *G. crassata,* (see Bandy 1964*a*).

In the Rakhi Nala material the final chamber is very often smaller than the penultimate and appears to be smoother than the earlier chambers. The periphery of the test varies from just spinose to distinctly keeled. The ornamentation of the umbilical shoulders and dorsal sutures is variable. The chambers in the last whorl often enlarge irregularly.

The present investigation does not support Bandy's (1964*a*) postulation that *G. crassata* is intermediate between *Globorotalia angulata* (White) and *Globorotalia rex* Martin.

As pointed out by Luterbacher (1965) the lectotype of *G. crassata* bears a close morphological resemblance to *Globorotalia marginodentata* Subbotina.

DISTRIBUTION. *Globorotalia crassata* was originally described from the Eocene of Mexico. In selecting the lectotype of *G. crassata* Bandy (1964*a*: 35) noted that 'Its exact range is not known; however, it appears to extend from the Upper Paleocene through the Lower Eocene into the Middle Eocene'. Banner & Blow (1965 : 113) correctly pointed out that 'the range of *G. crassata* given by Bandy (1964*a*, p. 35) is a synthesis of old and incorrect records, which do not apply to the lectotype'.

G. crassata has been recorded by the writer (1970*a*) from the Middle Eocene of Western India. In the Rakhi Nala section it occurs in the *Globorotalia crassata*/*Truncorotaloides topilensis* Zone.

Globorotalia ehrenbergi Bolli

(Pl. 13, figs 4–6)

1957*a* *Globorotalia ehrenbergi* Bolli: 77, pl. 20, figs 18–20.
1960*b* *Globorotalia ehrenbergi* Bolli; Bolli & Cita: 382–383, pl. 35, figs 4a–c.
1963 *Globorotalia ehrenbergi* Bolli; Dallan: 15–16, pl. 1, figs 3a–c.

REMARKS. The earlier chambers on the dorsal side may be slightly depressed below the outer whorl. The final chamber in some individuals is smaller than the penultimate. Although the present specimens agree quite well with the original description of *G. ehrenbergi,* the specimen figured here shows slightly more chambers in the last whorl than does the holotype, and has a more prominent apertural lip and weakly curved ventral sutures.

G. ehrenbergi is closely related to *Globorotalia compressa* (Plummer) from which it is thought to have been derived. Loeblich & Tappan (1957*a* : 188) considered the former to be a junior synonym of the latter, a view which Berggren (1962 : 96) regarded as unjustified.

Bolli (1957*a* : 77) remarked that 'Ehrenberg (1854) figured under *Planulina membranacea* the spiral views of 2 rotalid Foraminifera from the Cretaceous that are at least specifically different. Of these, one (pl. 26, fig. 43) could be near to a form subsequently described on several occasions as *Globorotalia membranacea* . . . No description or depository of a holotype was given by Ehrenberg however. It is for these reasons that a new name had to be chosen for these Paleocene specimens described as *Globorotalia membranacea*'. However, as pointed out by Loeblich & Tappan (1957*a* : 193) and accepted by others including Bolli & Cita (1960*b*), some of the keeled specimens from the Palaeocene earlier referred to *Globorotalia membranacea* (Ehrenberg) actually belong to *Globorotalia pseudomenardii* Bolli.

G. ehrenbergi resembles to *G. chapmani* Parr from which it differs in having more chambers, a less rapid enlargement of the chambers in the last whorl, a somewhat more compressed test and no 'imperforate' marginal band. McGowran (1968, pl.4, fig. 12) recently regarded *G. ehrenbergi* Bolli as a subspecies of *G. chapmani*.

Globorotalia haunsbergensis Gohrbandt (1963), described from the Palaeocene of Austria, was considered by Berggren & Olsson (1967 : 266) to be a junior synonym of *G. ehrenbergi*. Gohrbandt mentioned that *G. ehrenbergi* is distinguished from *G. haunsbergensis* essentially by the slower rate of the enlargement of the chambers and only slightly curved and more strongly depressed sutures on the dorsal side of the test. *G. haunsbergensis* is not here regarded as a synonym of *G. ehrenbergi*.

DISTRIBUTION. *G. ehrenbergi* was originally described from the Palaeocene, lower part of the Lizard Springs Formation of Trinidad and reported to range from the base of the *G. pusilla pusilla* Zone to the middle of the *G. pseudomenardii* Zone. Earlier, Subbotina (1953) had reported it as *Globorotalia membranacea* (Ehrenberg) from the Palaeocene of the Caucasus. It has also been reported from several other European localities.

In the Rakhi Nala section *G. ehrenbergi* occurs in the *Globorotalia velascoensis* Zone.

Globorotalia esnaensis (Le Roy)

(Pl. 15, figs 7–9)

1953 *Globigerina esnaensia* Le Roy: 31, pl. 6, figs 8–10.

REMARKS. The Rakhi Nala specimens show all the distinctive features of *G. esnaensis*. The main variation observed is in the degree of flattening of the dorsal side of the test, the shape and rate of enlargement of the chambers in the last whorl and the size of the aperture.

Le Roy (1953) compared *G. esnaensis* with *Globorotalia quadrata* (White) from which he distinguished the former by its roughened surface, more inflated last chamber and wider umbilicus. The two species, as represented in the Rakhi Nala material, are regarded as belonging to two distinctly different groups.

DISTRIBUTION. According to most authors this species ranges from the base of the Upper Palaeocene to the Lower Eocene. The writer (1970*c*) has examined abundant, well-preserved material of *G. esnaensis* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. esnaensis* ranges from the *Globorotalia aequa* Zone to the *Globorotalia aspensis*/*Globorotalia esnaensis* Zone.

Globorotalia formosa formosa Bolli

(Pl. 9, figs 1–3)

1957*a* *Globorotalia formosa formosa* Bolli: 76, pl. 18, figs 1–3

Remarks. Although the Rakhi Nala specimens agree satisfactorily with the original description and illustration of the subspecies, individuals with 8 chambers in the last whorl were not observed. The enlargement of the chambers in the last whorl may be irregular. Often the final chamber is smaller than the penultimate one. The sutures are incised round the umbilicus.

Distribution. The reported range of the subspecies is Upper Palaeocene to Lower Eocene. The writer has examined well-preserved, typical specimens of *G. formosa formosa* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. formosa formosa* occurs in the *Globorotalia formosa formosa* Zone.

Globorotalia formosa gracilis Bolli

(Pl. 11, figs 4–6)

1957*a* *Globorotalia formosa gracilis* Bolli: 75–76, pl. 18, figs 4–6.

Remarks. The main variation observed in the Rakhi Nala specimen is in the shape of the test in peripheral view, the rate of enlargement of the chambers in the last whorl and in the size of the umbilicus. The chambers in the last whorl may enlarge irregularly.

Bolli (1957*a* : 66) has indicated that *G. formosa gracilis* was probably derived from *G. aequa* Cushman & Renz.

Distribution. The range of this subspecies is reported to be Upper Palaeocene to Lower Eocene. The writer has examined well-preserved, typical specimens of *G. formosa gracilis* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. formosa gracilis* occurs in the *Globorotalia formosa formosa* Zone.

Globorotalia irrorata Loeblich & Tappan

(Pl. 14, figs 4–6)

1957*a* *Globorotalia irrorata* Loeblich & Tappan: 191, pl. 46, figs 2a–c; pl. 61, figs 5a–c.
1966 *Globorotalia irrorata* Loeblich & Tappan; El-Naggar: 216–217, pl. 23, figs 9a–c.

Remarks. The Rakhi Nala specimens agree most closely to *G. irrorata* Loeblich & Tappan to which they are assigned here. The specimen figured here compares well with the holotype of *G. irrorata*.

In the present material, *G. irrorata* shows a close resemblance to *Globorotalia quadrata* (White) from which it seems to have been derived by the development of the spinose surface.

In the course of his investigation on the Lower Eocene planktonic foraminifera from Denmark and northwestern Germany, Berggren (1960*a*) assigned specimens with roughly subcircular equatorial periphery, 5 chambers in the last whorl, wide umbilicus and umbilical aperture to Loeblich & Tappan's species which he transferred to the genus *Globigerina*. As pointed out by El-Naggar (1966 : 217) Berggren's figured specimen of *G. irrorata* differs distinctly from the holotype of *G. irrorata*.

Berggren (1960*a* : 67) remarked that it is questionable whether the paratype of *G. irrorata* figured by Loeblich & Tappan is conspecific with its holotype. As can be seen from the figures, the paratype differs from the holotype in lacking the small final chamber.

G. irrorata was compared by its authors with *Globigerina soldadoensis* Bronnimann and *Globorotalia convexa* Subbotina. These three species as represented in the present material are distinctly different from each other.

DISTRIBUTION. The holotype of *G. irrorata* was described from the Nanafalia Formation of Alabama, U.S.A., which was considered by Loeblich & Tappan (1957*a*, *b*) as Lower Eocene in age, but later studies have proved it to be Palaeocene. The paratype was described from the underlying Coal Bluff marl member of the Naheola Formation of Alabama. El-Naggar (1966) has reported *G. irrorata* as a rare to common form in the Upper Palaeocene of Nile Valley, Egypt.

In the Rakhi Nala section *G. irrorata* ranges from the *Globorotalia velascoensis* Zone to the *Globorotalia aspensis/Globorotalia esnaensis* Zone.

Globorotalia lehneri Cushman & Jarvis

(Pl. 14, figs 12–14)

1929 *Globorotalia lehneri* Cushman & Jarvis: 17, pl. 3, figs 16a–c.
1968 *Globorotalia lehneri* Cushman & Jarvis; Raju: 290, pl. 4, figs 1a–c.
1969 *Globorotalia lehneri* Cushman & Jarvis; Samanta: 334, pl. 2, figs 7a–c.
1970*a* *Globorotalia lehneri* Cushman & Jarvis; Samanta: 203, pl. 3, figs 13, 14.

REMARKS. The Rakhi Nala specimens are closely comparable to *G. lehneri* although individuals with radially elongated later chambers were not observed. The aperture appears to be furnished with a thin lip.

G. lehneri is distinguished from *Globorotalia spinulosa* Cushman by its compressed test, greater number of chambers in the last whorl, distinctly radially elongate later chambers and smoother surface. Bolli (1957*c* : 168) has suggested that *G. lehneri* was probably derived from *G. spinulosa*.

Globorotalia nagappai Raju (1968) described from the Lower Eocene *Globorotalia rex* to *Globorotalia palmerae* Zones of the Cauvery basin, southern India, shows strong affinities to *G. lehneri* although it differs in being smaller in size and in having fewer and more rapidly enlarging chambers in the last whorl.

DISTRIBUTION. *G. lehneri* had been reported from several areas including western India (Samanta 1970*a*), eastern India (Samanta 1969) and southern India (Raju 1968). According to most authors it is restricted to the Middle Eocene.

In the Rakhi Nala section *G. lehneri* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Globorotalia marginodentata Subbotina

(Pl. 11, figs 1–3)

1953 *Globorotalia marginodentata* Subbotina (pars): 212–213, pl. 17, figs 15a–16c; pl. 18, figs 2a–3c; non pl. 17, figs 14a–c; non pl. 18, figs 1a–c.

Remarks. The main variation in the Rakhi Nala specimen is in the shape of the test in peripheral view, the number of chambers in the last whorl, and in the size of the final chamber. The umbilicus is narrow and deep, and the umbilical shoulders are without special ornamentation.

Distribution. The range of the species is reported to be Upper Palaeocene to Lower Eocene. The writer has examined well preserved, typical representatives of *G. marginodentata* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. marginodentata* ranges from the *Globorotalia aequa* Zone to the *Globorotalia formosa formosa* Zone.

Globorotalia occlusa Loeblich & Tappan

(Pl. 10, figs 11–13)

1957*a* *Globorotalia occlusa* Loeblich & Tappan: 191, pl. 64, figs 3a–c; ?pl. 55, figs 3a–c.

Remarks. This taxon is used here in the sense of Hillebrandt (1962*b*), Gohrbandt (1963) and Luterbacher (1965).

The main variation observed in the Rakhi Nala material is in the shape of the test in peripheral view, the number and rate of enlargement of the chambers in the last whorl, and in the size of the umbilicus.

Distribution. According to most authors this species is restricted to the Upper Palaeocene. The writer (1970*c*) has examined well-preserved, abundant material of *G. occlusa* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. occlusa* occurs in the *Globorotalia velascoensis* and *Globorotalia aequa* Zones.

Globorotalia parva Rey

(Pl. 9, figs 4–6)

1955 *Globorotalia velascoensis* (Cushman) var. *parva* Rey: 209, pl. 12, figs 1a–b.

Distribution. *G. parva* is reported to be restricted to the Upper Palaeocene. The writer (1970*c*) has examined well-preserved typical representatives of *G. parva* from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. parva* occurs in the *Globorotalia velascoensis* and *Globorotalia aequa* Zones.

Globorotalia aff. ***primitiva*** (Finlay)

(Pl. 14, figs 9–11)

?1947 *Globoquadrina primitiva* Finlay: 291, pl. 8, figs 129–134.

REMARKS. The Rakhi Nala specimens are characterized by a low trochospirally coiled test; flattened dorsal side; strongly convex ventral side; subquadrate, lobate equatorial periphery; subrounded axial periphery; about $3\frac{1}{2}$ to 4 subglobular to subangular, rapidly enlarging chambers in the last whorl; straight to slightly curved sutures, deeply depressed on the ventral side, slightly depressed on the dorsal; small, deep umbilicus; coarsely spinose surface and low arched umbilical—extraumbilical aperture. The degree of flattening of the dorsal side of the test, angularity of the chambers in the last whorl and the size and shape of the final chamber show variation in the material. The final chamber is often strongly flattened and may be large enough in some specimens to occupy about half of the whole ventral side of the test. The umbilical region may be more coarsely ornamented than the rest of the test.

The present specimens differ from the types in lacking the mamillated surface and deeply incised sutures.

The present specimens also closely resemble *Globorotalia triplex* (Subbotina) described from the Palaeocene-Lower Eocene of Northern Caucasus, U.S.S.R. Gohrbandt (1963) has treated *G. triplex* as a junior synonym of *G. primitiva*.

DISTRIBUTION. *G. primitiva* was described by Finlay (1947) from the Middle Eocene of New Zealand where according to Jenkins (1966*a*), it ranges from his *G. triloculinoides* Zone, Palaeocene to his *G. inconspicua inconspicua* Zone, lower Upper Eocene.

In the Rakhi Nala section *G.* aff. *G. primitiva* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Globorotalia pseudobulloides (Plummer)

(Pl. 12, figs 1–3)

1926 *Globigerina pseudobulloides* Plummer: 133–134, pl. 8, figs 9a–c.

REMARKS. In the original description of *G. pseudobulloides* Plummer figured three specimens showing the dorsal, peripheral and ventral views respectively. She did not designate a holotype. Later, Loeblich & Tappan (1957*a*, pl. 44, figs 6a–c) illustrated three views of a topotype showing its morphology in detail.

The Rakhi Nala specimens show all the distinctive features of the species. The number and the rate of enlargement of the chambers in the last whorl, size of the final chamber and the height of the aperture all show variation. In the figured specimen the first chamber of the final whorl is partly damaged.

DISTRIBUTION. According to most authors, *G. pseudobulloides* ranges from the base of the Danian to the Upper Palaeocene. There are several reports of the species in the Indian region. The writer (1970*c*) has examined well-preserved, typical individuals from the Palaeocene Pondicherry Formation of southern India.

In the Rakhi Nala section *G. pseudobulloides* occurs in the *Globorotalia velascoensis* Zone.

Globorotalia pseudomenardii Bolli

(Pl. 13, figs 7–9)

1957*a* *Globorotalia pseudomenardii* Bolli: 77, pl. 20, figs 14–17.

Remarks. The Rakhi Nala specimens show all the distinctive features of *G. pseudomenardii*. The main variation observed is in the convexity of the dorsal side of the test, the degree of development of the peripheral keel and the rate of enlargement of chambers. Individuals with the final chamber smaller than the penultimate, and with a moderately lobate periphery occur.

Bolli (1957*a*) figured the holotype and the dorsal side of a paratype which was about twice as large. In the paratype the final chamber appears to be slightly smaller than the penultimate, and the equatorial periphery of the test is prominently lobate.

G. pseudomenardii is a very distinctive species. It differs from *G. chapmani* in having raised early chambers on the dorsal side of the test and a distinct peripheral keel. According to Bolli (1957*a*) *G. pseudomenardii* is closely related to *Globorotalia ehrenbergi* Bolli from which it seems to have been derived.

Distribution. *G. pseudomenardii* was first described from the lower part of the Lizard Springs Formation of Trinidad where it was found to be restricted to the *G. pseudomenardii* Zone. It has been reported from numerous other localities, and has been said to range through an interval corresponding to the combined *G. pseudomenardii* and *G. velascoensis* Zones of Bolli. The writer (1970*c*) has examined materials from the Pondicherry formation of southern India where *G. pseudomenardii* was found to range throughout the Upper Palaeocene.

In the Rakhi Nala section it occurs in the *Globorotalia velascoensis* Zone.

Globorotalia quadrata (White)

(Pl. 12, figs 4–6)

1928*a* *Globigerina quadrata* White: 195, pl. 27, figs 18a–b.

Remarks. White (1928*a*) figured only the ventral and dorsal views of a single specimen. His figures were of rather low magnification and the details of some features are not readily observed. He stated that the aperture was obscured. To the best of the writer's knowledge, no attempt has since been made to discuss and demonstrate in detail the morphological characteristics and the variability of the species either in the type or in topotypic material.

Bolli (1957*a*) assigned specimens with an extra-umbilical-umbilical aperture to this species which he accordingly transferred to the genus *Globorotalia*, a change accepted by later workers.

In the Rakhi Nala material, the main variation is in the rate of enlargement of the chambers in the last whorl and the shape and size of the final chamber. The four chambers in the last whorl may be subequal in size. Often the final chamber is smaller than the penultimate in size.

G. quadrata is readily distinguished from *Globorotalia pseudobulloides* (Plummer) by its fewer less rapidly enlarging and more tightly arranged chambers in the last whorl, the quadrate equatorial outline of the test and the character of the intercameral sutures.

The two specimens from the basal Laki of Western Pakistan identified by Haque (1956, pl. 26, figs 7–8) as *Globigerina quadrata* White are inadequately illustrated and do not show the distinctive features of the species.

DISTRIBUTION. White (1928*a* : 195) described *G. quadrata* from the Tampico Embayment of Mexico where Hay (1960) found it to range from the *Globigerinoides daubjergensis* Subzone, lower part of the Velasco Formation to the *Globorotalia velascoensis* Zone, top of the Velasco Formation. The writer (1970*c*) has examined well-preserved, typical representatives from the Palaeocene Pondicherry formation of southern India.

In the Rakhi Nala section *G. quadrata* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis/Globorotalia esnaensis* Zones.

Globorotalia quetra Bolli

(Pl. 10, figs 5–7)

1957*a* *Globorotalia quetra* Bolli: 79–80, pl. 19, figs 1–6.
1961 *Pseudogloborotalia quetra* (Bolli); Bermudez: 1348.
1962*b* *Globorotalia* (*Acarinina*) *quetra* Bolli; Hillebrandt: 144, pl. 14, figs 2a–c.
1965 *Acarinina quetra* (Bolli); Hillebrandt: 17.

REMARKS. The Rakhi Nala specimens agree well with the original definition of the species. The chambers in the last whorl are elongated in the direction of coiling. The later chambers are usually peripherally flattened. The intensity of the surface ornamentation varies. The dorsal side of the test appears to be less spinose than the ventral. As pointed out by Bolli (1957*a*) *G. quetra* bears a close morphological resemblance to the *Truncorotaloides rohri-topilensis* group of forms. However, the sutural opening on the dorsal side of the test, the characteristic feature of the representatives of the genus *Truncorotaloides*, is lacking in *G. quetra*.

Bolli distinguished *G. quetra* from *Globorotalia wilcoxensis* Cushman & Ponton by the distinct angular shape of the test. He reported the occurrence of forms intermediate between these two species in the lower part of the Upper Lizard Springs formation of Trinidad. *Globorotalia whitei* Weiss was regarded by Bolli as the ancestral form of *G. quetra*.

The specimen from the Lower Eocene of Caucasus, U.S.S.R. figured by Subbotina (1953, pl. 22, figs 1a–c) as *Acarinina pseudotopilensis* strongly resembles *G. quetra* in possessing subangular, peripherally flattened chambers in the last whorl, and a coarsely spinose surface. The chambers are elongated in the direction of coiling.

According to El-Naggar (1966 : 192) some specimens with weak marginal keels described by Loeblich & Tappan (1957*a*) as *Globorotalia aequa* Cushman & Renz probably belong to *G. quetra* Bolli.

DISTRIBUTION. *Globorotalia quetra* was described by Bolli (1957*a*) from the Lower Eocene, Upper Lizard Springs formation of Trinidad. Its reported range is Upper Palaeocene to Lower Eocene.

In the Rakhi Nala section *G. quetra* ranges from the Upper Palaeocene *Globorotalia aequa* Zone to the Lower Eocene *Globorotalia formosa formosa* Zone.

Globorotalia renzi Bolli

(Pl. 13, figs 10–12)

1957*c* *Globorotalia renzi* Bolli: 168, pl. 38, figs 3a–c.

REMARKS. The specimen figured here closely resembles the holotype. With its compressed biconvex test, smooth surface and thin peripheral keel, *G. renzi* is readily distinguished from contemporaneous species in the Rakhi Nala material.

In his original description, Bolli compared *G. renzi* only with *Globorotalia lehneri* Cushman & Jarvis. In the writer's view these two species belong to different groups.

DISTRIBUTION. Originally described from the Middle Eocene of Trinidad by Bolli, the species is reported to range from Lower to Middle Eocene. The writer (1970*a*) has recorded *G. renzi* from the Middle Eocene *Orbulinoides beckmanni* and *Truncorotaloides rohri* Zones of western India.

In the Rakhi Nala section *G. renzi* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globorotalia spinuloinflata (Bandy)

1949 *Globigerina spinuloinflata* Bandy: 122, pl. 23, figs 1a–c.
1968 *Globorotalia spinuloinflata* (Bandy); Raju: 290, pl. 3, figs 1a–b.
1969 *Globorotalia spinuloinflata* (Bandy); Samanta: 335, pl. 2, figs 5a–c.
1970*a* *Globorotalia spinuloinflata* (Bandy); Samanta: 204, pl. 3, figs 1–4.

REMARKS. The Rakhi Nala specimens show all the diagnostic features of the species. *Globorotalia crassata* var. *densa* (Cushman), first described from Mexico, may be closely related to *G. spinuloinflata*. However, the absence of an illustration in the original publication of Cushman's form does not permit a proper comparison with the present species.

DISTRIBUTION. This species is reported to range from the Lower Eocene to the upper Middle Eocene. It has been reported from the Middle Eocene of eastern India (Samanta 1969), western India (Samanta 1970*a*) and southern India (Raju 1968).

In the Rakhi Nala section *G. spinuloinflata* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globorotalia spinulosa Cushman

(Pl. 14, figs 1–3)

1927 *Globorotalia spinulosa* Cushman: 114, pl. 23, figs 4a–c.
1969 *Globorotalia spinulosa* Cushman; Samanta: 335, pl. 2, figs 6a–c.
1970*a* *Globorotalia spinulosa* Cushman; Samanta: 204, pl. 3, figs 7–8.

REMARKS. In the present material this species shows variation in the shape of the dorsal side of the test, the number and rate of enlargement of the chambers in the last whorl, and in the intensity of the surface ornamentation. The earlier chambers may be more coarsely ornamented than the later ones. The spines along the periphery of the test, when close spaced, produce a keel-like structure The final chamber may constitute about one-third of the ventral side of the test. The specimen figured here closely resembles the illustrations of the holotype.

When commenting on Bandy's (1964*a*) selection of a lectotype for *Globorotalia crassata* (Cushman), Banner & Blow (1965 : 113) wrote: 'Bandy's lectotype . . . is virtually identical to Bolli's hypotypes of *Globorotalia spinulosa* (Bolli, 1957*a*, p. 168, pl. 38, figs 6, 7) and is very similar indeed to the holotype of *G. spinulosa* as originally figured by Cushman, 1927. Thus, as a result of Bandy's work, it can be seen that *G. crassata* (Cushman, 1925) is a prior synonym of *G. spinulosa* Cushman, 1927'.

Globorotalia spinulosa can be satisfactorily distinguished from *G. crassata* by its smaller, more delicate test; fewer, and more rapidly enlarging chambers in the last whorl; narrower umbilicus and weaker peripheral ornamentation.

DISTRIBUTION. *Globorotalia spinulosa* was first described from the 'Upper Eocene Alazan Clay' of Mexico. In well-described sections *G. spinulosa* does not range above the Middle Eocene. The reports of its occurrence in the Lower Eocene need verification. The writer (1969 and 1970*a*) has recorded *G. spinulosa* from the Middle Eocene of eastern India and western India.

In the Rakhi Nala section *G. spinulosa* occurs in the *Globorotalia crassata*/*Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Globorotalia subbotinae Morozova

(Pl. 10, figs 14–16)

1939 *Globorotalia subbotinae* Morozova: 80, pl. 2, figs 16–17.

REMARKS. The Rakhi Nala specimens show all the distinctive features of *G. subbotinae*. The main variation observed is in the shape of the dorsal side of the test, the number and rate of the enlargement of the chambers in the last whorl and the intensity of the surface ornamentation, especially along the periphery.

The two specimens from the *Globorotalia rex* Zone of the Cauvery Basin, southern India, figured by Raju (1968, pl. 3, figs 4a–5) as *G. rex* Martin show some resemblance to *G. subbotinae*.

DISTRIBUTION. The recorded range of *G. subbotinae* is Upper Palaeocene to Lower Eocene. The writer (1970*c*) has examined well preserved material of *G. subbotinae* from the Palaeocene Pondicherry Formation of southern India.

In the Rakhi Nala section *G. subbotinae* ranges from the *Globorotalia aequa* Zone to the *Globorotalia formosa formosa* Zone.

Globorotalia tadjikistanensis Bykova

(Pl. 8, figs 10–12)

1953 *Globorotalia tadjikistanensis* Bykova: 86, pl. 3, figs 5a–c.
1965 *Globorotalia tadjikistanensia* Bykova; Luterbacher: 663–665, text-figs 52a–c.

Remarks. The Rakhi Nala specimens show most of the distinctive features of *G. tadjikistanensis*, although a specimen like the holotype, i.e. with about 8 chambers in the last whorl, was not observed.

G. tadjikistanensis shows some resemblance to *G. conicotruncata* Subbotina, but is readily distinguished by the biconvexity of its test. Subbotina's form also possesses a more acute axial periphery, often with a faint keel, and usually has a more distinctly developed umbilicus.

Bykova's species differs from *G. angulata* in having more chambers in the last whorl and in the convexity of the dorsal side of the test. The chambers in the last whorl also enlarge more slowly than in *G. angulata*. According to Bykova, *G. tadjikistanensis* was derived directly from *G. angulata*.

The biconvex test of *G. tadjikistanensis* also resembles *Globorotalia simulatilis* (Schwager) as discussed and illustrated by Luterbacher (1965). The latter is distinguished by having fewer chambers in the last whorl and usually in being less convex dorsally.

Distribution. *G. tadjikistanensis* was originally described from the *Globorotalia tadjikistanensis* Zone in Central Asia. It was reported by Leonov & Alimarina (1961) from the Palaeocene, *Globorotalia conicotruncata*/*Globorotalia tadjikistanensis* Zone of the Caucasus. Luterbacher (1965) reported it from the Gubbio section of Central Italy where he found it to range from the middle of the *Globorotalia pusilla pusilla* Zone to the middle of the *G. pseudomenardii* Zone.

In the Rakhi Nala section *G. tadjikistanensis* occurs in the *Globorotalia velascoensis* Zone.

Globorotalia troelseni Loeblich & Tappan

(Pl. 13, figs 1–3)

1957*a* *Globorotalia troelseni* Loeblich & Tappan: 196, pl. 60, figs 4a–c; pl. 63, figs 5a–c.
1957*a* *Globorotalia elongata* Glaessner; Bolli: 77, pl. 20, figs 11–13.

Remarks. This species is distinguished from its close relatives in the Rakhi Nala material by its distinctly elongate test, greater number of chambers in the last whorl, and tendency to become evolute.

In the original description, Loeblich & Tappan figured the holotype and one paratype. The large subcircular opening in the holotype appears to be a foramen and the final chamber seems not to be preserved. The prominent keel-like structure shown in the peripheral view of the holotype is somewhat unusual in this group of forms. In contrast to the holotype, the paratype shows a subacute axial periphery without a keel, and the earlier whorls are not visible within the umbilicus.

Gohrbandt (1967*a*) and Berggren & Olsson (1967) considered *G. troelseni* to be a junior synonym of *G. chapmani* Parr. However, the former differs in having a more elongate test, more, but less rapidly enlarging, chambers in the last whorl, in its tendency towards evolute coiling in the last whorl, and in lacking an 'imperforate' marginal band.

In its elongate test, about 6 slowly enlarging chambers in the last whorl, depressed early spire on the dorsal side and subacute axial periphery, Bolli's (1957*a*) figured specimen of *Globorotalia elongata* Glassener from the *G. pseudomenardii* Zone of Trinidad seems to fall within the range of variation of *G. troelseni*. It closely resembles the figured paratype.

Berggren's (1960*c*, pl. 1, figs 21a–c) figured specimen of *G. troelseni* from the Upper Palaeocene of Nigeria shows a more rounded axial periphery but is otherwise similar to the types.

The holotype of *Globorotalia emilei* El-Naggar resembles very closely the figured paratype of *G. troelseni*. However, El-Naggar did not compare his species with *G. troelseni*, and an examination of well-preserved material of *G. emilei* is needed to establish their relationships.

The specimen from the Palaeocene of Austria figured by Gohrbandt (1963, pl. 6, figs 13–15) as *G. troelseni* shows all the distinctive features of *G. chapmani* to which I think it belongs.

The preservation of the specimen from the Esna-Idfu region of Egypt recorded by El-Naggar (1966, pl. 17, figs 10a–c) as *G. troelseni* is not satisfactory enough to make definite remarks about its identification.

DISTRIBUTION. The holotype of *G. troelseni* was described from the Nanafalia formation of Alabama and the figured paratype from the Velasco formation of Mexico. Some records of *G elongata* Glaessner seem to refer to *G. troelseni*. This species apparently ranges from Middle to Upper Palaeocene.

In the Rakhi Nala section, *G. troelseni* occurs in the *Globorotalia velascoensis* Zone.

Globorotalia varianta (Subbotina)

(Pl. 12, figs 7–9)

1947 *Globigerina pseudobulloides* Plummer; Subbotina: 106–107, pl. 4, figs 8–10.
1953 *Globigerina varianta* Subbotina (pars): 63–64, pl. 3, figs 5a–7c, 9a–12c; pl. 4, figs 1a–3c; ?pl. 15, figs 1a–3c; *non* pl. 3, figs 8a–c.
1957*a* *Globigerina triloculinoides* Plummer; Bolli (pars): 70, pl. 17, figs 25–26; *non* pl. 15, figs 18–20.
1962*b* *Globorotalia* (*Globorotalia*) *varianta* (Subbotina); Hillebrandt: 125, pl. 12, figs 10a–11b.
1963 *Globigerina pseudobulloides varianta* Subbotina; Gohrbandt: 45, pl. 1, figs 16–18.
1965 *Globorotalia varianta* (Subbotina); Berggren: 295–196, text-fig. 12a–c.

REMARKS. Subbotina (1953) illustrated fourteen specimens in her original description. Of these, one (pl. 3, figs 8a–c) has a spinose surface and three others (pl. 15) have abnormal final chambers. These four should not be assigned to *G. varianta* in the opinion of the present author.

Because of its extraumbilical-umbilical aperture the species was removed by later workers from the genus *Globigerina* to *Globorotalia.*

The Rakhi Nala specimens show all the distinctive features of *G. varianta.* However, the aperture is slightly higher in these specimens than in the holotype and figured paratypes. Individuals with slightly less than 4 chambers in the last whorl are present. Often the final chamber tends to be radially elongate. The surface of the test is usually finely perforate.

As observed by Subbotina (1953), *G. varianta* is morphologically very similar to *Globorotalia pseudobulloides* (Plummer). Earlier, (1947) she included a specimen of *G. varianta* in *G. pseudobulloides.* Gohrbandt (1963) treated *G. varianta* as a subspecies of *G. pseudobulloides,* while Berggren (1962) and El-Naggar (1966) regarded it as a junior synonym of *G. pseudobulloides.* However, as noted by some previous authors the two species are morphologically and stratigraphically distinct.

Gohrbandt (1963 : 45) suggested that *Globorotalia quadrata* (White) (=*Globigerina quadrata*) may be senior synonym of *G. varianta.* Specimens transitional between them occur in the Rakhi Nala material.

As pointed out by Gohrbandt (1963), Bolli's (1957*a*, pl. 17, figs 25–26) figured specimen of *Globigerina triloculinoides* Plummer from the Palaeocene of Trinidad should be placed in synonymy with *G. varianta.*

The prominently spinose specimens with 5–6 chambers in the last whorl which Loeblich & Tappan (1957*a*) identified as *G. varianta* are here regarded as a different species.

The specimen figured by Berggren (1965, text-fig. 12a–c) from the Mexia Clay of Texas differs from the holotype in having a less tightly coiled test, a wider umbilicus and a higher aperture.

Berggren's (1965) statement that Said & Kerdany's (1961, pl. 1, figs 3a–c) figured specimen of *Globigerina eocaena* Gümbel from the Palaeocene of Egypt belongs to *G. varianta* is not accepted here. The Egyptian specimen differs from *G. varianta* in having slowly enlarging and less inflated chambers, and a subrounded to subangular axial periphery.

DISTRIBUTION. *G. varianta* was first described from the Zone of Rotalia-like Globorotalias, Elburgan horizon, of the Caucasus. Subbotina (1953) gave the range as ?Danian to Middle Eocene. This long stratigraphic range has not been accepted by later workers.

G. varianta is widely distributed and has been reported from the Palaeocene of Austria, Trinidad, U.S.A. and North Africa. According to most workers it ranges from the Palaeocene to the Lower Eocene.

In the Rakhi Nala section *G. varianta* ranges from the *Globorotalia velascoensis* Zone to the *Globorotalia aspensis/Globorotalia esnaensis* Zone.

Globorotalia velascoensis (Cushman)

(Pl. 9, figs 7–9)

1925*b* *Pulvinulina velascoensis* Cushman: 19, pl. 3, figs 5a–c.
1956 *Globorotalia velascoensis* (Cushman); Haque: 181, pl. 24, figs 2a, b.
1970*c* *Globorotalia velascoensis* (Cushman); Samanta: 636, pl. 97, figs 7–10.

Remarks. The main variation observed in the Rakhi Nala material is in the number and rate of enlargement of the chambers in the last whorl, the degree of lobation of the equatorial periphery, the size of the umbilicus, and the degree of ornamentation. With its large, planoconvex, multichambered test; wide, open umbilicus and heavily ornamented umbilical shoulders, peripheral keel and dorsal sutures, *G. velascoensis* is one of the most conspicuous and readily recognizable planktonic foraminifera in the present material.

Distribution. According to most authors *G. velascoensis* is restricted to the Upper Palaeocene. The writer (1970*c*) has examined well-preserved typical and abundant representatives of *G. velascoensis* in the Palaeocene Pondicherry Formation of South India.

In the Rakhi Nala section *G. velascoensis* occurs in the *Globorotalia velascoensis* and *Globorotalia aequa* Zones.

Globorotalia whitei Weiss

(Pl. 15, figs 1–3)

1955*a* *Globorotalia whitei* Weiss: 18–19, pl. 6, figs 1–3.

Remarks. The specimen figured here closely resembles the holotype. As in the holotype, the ventral sutures form an X-shaped pattern and the final chamber is about twice the size of the penultimate chamber.

Weiss (1955*a*) pointed to the resemblance between *G. whitei* and *Globorotalia crassula* Cushman & Stewart, described from the Pliocene of California. He did not compare it with the morphologically similar contemporaneous forms of the genus, neither did he discuss the range of variation in the type material. These deficiencies might have made its identification difficult for later authors.

Distribution. The range of *G. whitei* is reported to be Palaeocene to Lower Eocene. The writer (1970*c*) has examined abundant well-preserved specimens from the Palaeocene Pondicherry Formation of southern India.

In the Rakhi Nala section *G. whitei* ranges from the *Globorotalia velascoensis* Zone to the *Globorotalia formosa formosa* Zone.

Globorotalia wilcoxensis Cushman & Ponton

1932 *Globorotalia wilcoxensis* Cushman & Ponton: 71, pl. 9, figs 10a–c.
1949 *Globorotalia* (*Truncorotalia*) *wilcoxensis* Cushman & Ponton; Cushman & Bermudez: 39, pl. 7, figs 16–18.
1956 *Globorotalia wilcoxensis* Cushman & Ponton; Haque: 183, pl. 4, figs 6a–c.
1957*a* *Globorotalia wilcoxensis* Cushman & Ponton; Bolli: 79, pl. 19, figs 7–9.

Remarks. In their original description, Cushman and Ponton mentioned that there are 4 chambers in the last whorl, although their figures of the holotype show clearly about 4½ chambers in the last whorl. The aperture as shown in the peripheral view of the holotype does not extend much outside the umbilicus. The last two chambers were almost the same in size. The variability of *G. wilcoxensis* in the type material was not discussed by its authors.

G. wilcoxensis and *G. whitei* Weiss are very closely related. Gohrbandt (1963) regarded *G. whitei* as a junior synonym of *G. wilcoxensis*, while Bolli (1957*a*) regarded *G. whitei* as the ancestral form of *G. wilcoxensis*.

DISTRIBUTION. *G. wilcoxensis* was originally described from the Lower Eocene of Alabama. In Trinidad, Bolli (1957*a*) found it to be restricted to the lower part of the upper Lizard Springs Formation. The range of the species is reported to be Palaeocene to Upper Eocene. Records of this species from the Middle and Upper Eocene require verification. The illustrations of the specimen (or specimens, as the two figures differ in size) from the Middle Eocene, of Mississippi provided by Cushman & Todd (1948, pl. 6, figs 24–25) are not adequate for satisfactory identification. Bermudez (1961 : 1351) pointed out that earlier records of Upper Eocene occurrences of *G. wilcoxensis* are doubtful.

In the Rakhi Nala section *G. wilcoxensis* ranges from the *Globorotalia aequa* Zone to the *Globorotalia formosa formosa* Zone.

Genus ***TRUNCOROTALOIDES*** Bronnimann & Bermudez 1953

TYPE SPECIES. *Truncorotaloides rohri* Bronnimann & Bermudez 1953.

See Samanta (1969) for discussion of genus.

Truncorotaloides collactea (Finlay)

(Pl. 7, figs 13–15)

1939*b* *Globorotalia collactea* Finlay: 327, pl. 29, figs 164–165.
1970*a* *Truncorotaloides collactea* (Finlay); Samanta: 205, pl. 3, figs 15–17.

REMARKS. In the Rakhi Nala material the dorsal sutural openings are too minute to be observed readily. The main variation observed is in the shape of the chambers in the last whorl, lobation of the equatorial periphery and the surface ornamentation of the test. Individuals with subangular chambers are rare.

According to Jenkins, *T. collactea* is possibly related to *T. rohri* Brönnimann & Bermudez, but differs in having a smaller and more compact test, much smaller dorsal sutural openings and a less spinose surface.

DISTRIBUTION. The range of *T. collactea* is reported to be Lower Eocene to lower Upper Eocene. The writer (1970*a*) has reported it from the Middle Eocene of western India.

In the Rakhi Nala section, *T. collactea* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Truncorotaloides rohri Brönnimann & Bermudez

(Pl. 6, figs 11–12)

1953 *Truncorotaloides rohri* Brönnimann & Bermudez: 818–819, pl. 87, figs 7–9.
1968 *Truncorotaloides rohri* Brönnimann & Bermudez; Raju: 290, pl. 2, figs 3a–c.
1970*a* *Truncorotaloides rohri* Brönnimann & Bermudez; Samanta: 207, pl. 3, figs 20–21.

REMARKS. The Rakhi Nala specimens show all the diagnostic features of the species. The dorsal sutural openings are observed in well-preserved specimens.

Distribution. *Truncorotaloides rohri* is believed to be restricted to the Middle Eocene. Raju (1968) has recorded it from bore holes in southern India, and it has been reported by the writer (1969, 1970*a*) from the Middle Eocene of eastern and western India.

In the Rakhi Nala section *T. rohri* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Truncorotaloides topilensis (Cushman)

(Pl. 6, figs 9–10)

1925*a* *Globigerina topilensis* Cushman: 7, pl. 1, figs 9a–c.
1968 *Truncorotaloides topilensis* (Cushman); Raju: 290, pl. 2, figs 9a–c.

Remarks. The Rakhi Nala specimens show all the distinctive features of the species. The specimen figured here is more tightly coiled than the holotype.

Distribution. In the original description it was stated that the holotype was obtained from the 'Upper Eocene, Tantoyuca formation, yellow clay from Palacho Hacienda, S. of Panuco—Tampico R. R., State of Vera Cruz, Mexico'. However, according to Barker (quoted in Blow & Saito 1968) the original age determination of the specimens described from the Palacho Hacienda area was not reliable as Cushman's sample was probably obtained from a derived block in the post-Eocene beds.

T. topilensis is believed to be restricted to the Middle Eocene. The writer (1969, 1970*a*) has recorded it from the Middle Eocene of eastern and western India. Raju (1968) has reported it from southern India.

In the Rakhi Nala section *T. topilensis* occurs in the *Globorotalia crassata/Truncorotaloides topilensis* Zone.

Family **HANTKENINIDAE** Cushman 1927

Genus ***HANTKENINA*** Cushman 1925

Type species. *Hantkenina alabamensis* Cushman 1925.
See Samanta (1969) for discussion of genus.

Hantkenina dumblei Weinzierl & Applin

(Pl. 7, fig. 18)

1929 *Hantkenina dumblei* Weinzierl & Applin: 402, pl. 43, figs 5a–b.
1939 *Hantkenina cf. dumblei* Weinzierl & Applin; Cushman & Siegfus: 32, pl. 7, fig. 2.
1942 *Hantkenina* (*Applinella*) *dumblei* Weinzierl & Applin; Thalmann: 812, pl. 1, figs 2a–b (after Weinzierl & Applin 1929).
1950 *Hantkenina* (*Applinella*) *dumblei* Weinzierl & Applin; Brönnimann: 408–410, pl. 55, figs 18, 22–24.
1958 *Hantkenina* (*Applinella*) cf. *dumblei* Weinzierl & Applin; Crespin (pars): 318, text-figs 3–4, ?1–2.
1966 *Hantkenina aragonensis* Nuttall; Premoli Silva & Luterbacher: 1192, text-fig. 5.
1968 *Hantkenina dumblei* Weinzierl & Applin; Raju; 290, pl. 1, fig. 5.

Remarks. The original illustrations of *Hantkenina dumblei* were the side views of two specimens. Of these, the smaller was regarded as a young specimen and the larger as a more mature form. The latter was designated lectotype by Brönnimann (1950).

Bolli, Loeblich & Tappan (1957) examined and refigured both the lectotype and the paratype of *H. dumblei* and remarked that 'The final chamber is broken from the lectotype of *H. dumblei*, but the remnants of this final chamber show an attachment partially enveloping the base of the spine of the penultimate chamber'. However, an examination of their figures shows that it is not in the lectotype (fig. 6) but in the paratype of *H. dumblei* that the final chamber is not preserved. As can be seen from the side view, the lectotype seems to possess a partially damaged apertural face. Neither Weinzierl & Applin nor Bolli, Loeblich & Tappan provided an illustration showing the apertural view of the lectotype. Although the preservation of both the lectotype and the figured paratype of *H. dumblei* is not completely satisfactory, they show adequately the characteristic features of the species.

The Rakhi Nala specimens agree satisfactorily with the original description and illustration of *Hantkenina dumblei*. The earlier chambers in the last whorl are slightly separated peripherally, and the later chambers are roughly triangular in side view. In the specimen figured here each chamber is about double the size of the previous chamber, the final chamber forming about one-third of the test. The spines which are only partly preserved, shift towards the anterior suture during ontogenesis. The surface of the test is smooth except for the first two chambers of the last whorl which are hispid. The aperture is an elongate arched opening with a tendency to develop besal lobes. It extends up to about half the height of the apertural face and is furnished with distinctly developed lateral lip-like projections. In all the three specimens the aperture is filled up with recrystallized material.

H. dumblei was designated type species for the subgenus *Applinella* Thalmann. However, the writer does not accept subgeneric divisions of the genus *Hantkenina* (see Samanta 1969).

H. dumblei is similar to *H. longispina* Cushman but is distinguished by its more elongate chambers and shorter and more slender spines.

According to Brönnimann (1950) *H. dumblei* was probably derived from *H. mexicana* Cushman.

The two specimens from the Navet formation of Trinidad illustrated by Brönnimann (1950, pl. 55, fig. 17; pl. 56, fig. 5) as *Hantkenina* (*Applinella*) cf. *dumblei* differ from Weinzierl & Applin's form in having peripherally separated later chambers with the spines not directly situated below the anterior suture.

The specimens from Italy illustrated by Premoli Silva & Luterbucher (1966, text-fig. 5) as *Hantkenina aragonensis* Nuttall show about 5 to 6 rapidly enlarging chambers in the last whorl; these are not distinctly separated peripherally and the spines are situated directly below the anterior suture.

Distribution. *Hantkenina dumblei* was originally described from the Middle Eocene of Texas. It was later recorded from California, Trinidad, several European localities, North Africa, southern India, Japan, Borneo and Australia. According to most authors the species is restricted to the Middle Eocene. Its reported occurrence in the Upper Eocene and in the basal Oligocene of Morocco (Rey 1939) is not reliable (see Thalmann 1942 : 818).

In the Rakhi Nala section *H. dumblei* occurs in the *Globorotalia crassata/ Truncorotaloides topilensis* Zone.

Hantkenina mexicana Cushman

(Pl. 7, figs 16–17)

1925*c* *Hantkenina mexicana* Cushman: 3, pl. 2, fig. 2.
1953 *Hantkenina mexicana* Cushman var. *aragonensis* Nuttall; Hamilton: 229, pl. 32, fig. 18, ?17.
1968 *Hantkenina mexicana* Cushman; Raju: 290, pl. 1, fig. 1.
1968 *Hantkenina aragonensis* Nuttall; Raju: 290, pl. 1, figs 2, 8.

REMARKS. Only five specimens were observed in the Rakhi Nala material and their preservation is not very good. However, the presence of peripherally well separated chambers with the spines situated in the prolongation of the chamber axis permits their satisfactory identification. The aperture is not preserved. The final chamber differs from the rest in being much more elongate.

H. mexicana is a very distinctive species. It is easily distinguished from other species of the genus by its peripherally well separated elongate chambers tapering more or less gradually into the terminal spines situated in the prolongation of the chamber axis. The rate of enlargement of the chambers, the degree of lobation of the periphery, the length of the spines and the shape of the chambers all vary.

Hamilton (1953, pl. 32, figs 17–18) figured two specimens from the Pacific Seamounts as *H. mexicana* Cushman var. *aragonensis* Nuttall. One (Figure 17) differs from typical *N. mexicana* in having narrower, much elongated and almost cylindrical chambers which are widely separated peripherally. It bears a striking resemblance to some specimens of *Clavigerinella jarvisi* figured by Cushman (1930, pl. 3, figs 8–11) from Trinidad.

In its elongated chambers deeply separated from each other at the periphery, *H. mexicana* bears close resemblance to *H. lehneri* Cushman & Jarvis. The specimen from Tanganyika figured by Ramsay (1962, pl. 16, fig. 2) as *H. lehneri* appears to be transitional between *H. mexicana* and *H. lehneri*.

H. mexicana is the earliest species of the genus. According to Berggren & Olsson (1967) it probably evolved from a form such as *Clavigerinella* aff. *akersi* Bolli, Loeblich & Tappan illustrated by Bolli (1957*c*, pl. 35, figs 3a–b) from the Navet Formation of Trinidad.

DISTRIBUTION. *H. mexicana* has been reported from numerous areas including western India and southern India. According to most workers it is restricted to the Middle Eocene.

In the Rakhi Nala section *H. mexicana* occurs in the *Globorotalia crassata/ Truncorotaloides topilensis* Zone.

Genus ***PSEUDOHASTIGERINA*** Banner & Blow 1959

TYPE SPECIES. *Nonion micrus* Cole 1927.
See Samanta (1969) for discussion.

Pseudohastigerina danvillensis (Howe & Wallace)

(Pl. 7, figs 7–8)

1932 *Nonion danvillensis* Howe & Wallace: 51–52, pl. 9, figs 3a–b.
1939 *Nonion danvillensis* Howe & Wallace; Cushman: 5, pl. 1, figs 19a–b.
1945 *Nonion danvillensis* Howe & Wallace; Cushman & Todd: 92, pl. 15, fig. 4.
1960*c* *Hastigerina danvillensis* (Howe & Wallace); Berggren: 85–86.

REMARKS. In the original figure of the holotype Howe & Wallace showed a papillate 'filling' in the umbilicus. However, they did not mention it in their description. Bandy (1949) in assigning specimens from the Eocene of Alabama to *Nonion danvillensis*, used this feature as one of the diagnostic characters. On the other hand, Cushman (1939) and Barker (quoted in Berggren 1960*a* : 86), who examined topotype material did not mention a pillate umbilicus. An examination of the holotype is needed to ascertain whether or not it possesses a truly papillate umblicus. Matrix in the umbilical depression could give the appearance of papillate ornamentation. Following Berggren's (1960*a*) observations, *N. danvillensis* is here assigned to *Pseudohastigerina*.

The degree of evoluteness of the test, the compression of the chambers, the lobation of the periphery and the height of the aperture vary in the material. Often the later chambers are much compressed producing an angular periphery.

P. danvillensis is closely related to *P. micra* (Cole) from which it is distinguished by its more numerous chambers in the last whorl, higher aperture, more compressed chambers and the tendency to evolute coiling. It seems to have been derived from *P. micra*.

DISTRIBUTION. This species was originally described from the Upper Eocene of Louisiana. It was later reported from the Lower Oligocene of Alabama (Howe 1942) and from several other Upper Eocene localities in North America.

In the Rakhi Nala section *P. danvillensis* ranges from the upper part of the *Truncorotaloides rohri* Zone to the *Globigerina officinalis* Zone.

Pseudohastigerina micra (Cole)

(Pl. 7, figs 11–12)

1927 *Nonion micrus* Cole: 22, pl. 5, fig. 12.

REMARKS. The number and degree of inflation of the chambers in the last whorl, and the height of the aperture vary in this material.

The axial periphery of the test may be almost subangular. The surface of the early chambers in the last whorl is very often weakly hispid.

Pseudohastigerina iota (Finlay), regarded by Berggren (1960*a* : 86) as a junior synonym of *P. micra*, can be distinguished by its fewer and more rapidly enlarging chambers in the last whorl, and its higher aperture. The two also differ in their stratigraphic ranges.

Distribution. *Pseudohastigerina micra* was originally described from the Middle Eocene of Mexico. According to Blow & Banner (1962), its range is Middle Eocene to Middle Oligocene.

In the Rakhi Nala section it ranges from the *Globorotalia crassata/Truncorotaloides topilensis* Zone to the *Globigerina officinalis* Zone.

Pseudohastigerina pseudoiota (Hornibrook)

(Pl. 7, figs 3–4)

1958*a* *Globigerina pseudoiota* Hornibrook: 34, pl. 1, figs 16–18.
1958*b* *Globigerina pseudoiota* Hornibrook; Hornibrook: 664–665, figs 23, 26–28.
1967 *Pseudohastigerina wilcoxensis* (Cushman & Ponton); Berggren & Olsson: 278–280, text-fig. 5 (1a–9c).

Remarks. While describing this species, Hornibrook (1958*a*) noted its 'striking resemblance to the small group of planispiral Eocene species of "*Globigerinella*" '. He (1958*b*) stressed the distinctly asymmetrical coiling and aperture, and the inflated rounded shape of the chambers.

Berggren & Olsson (1967), in discussing the development of *Pseudohastigerina* Banner & Blow, regarded *P. pseudoiota* as a junior synonym of *P. wilcoxensis* (Cushman & Ponton). The writer accepts these as congeneric but not conspecific. *P. pseudoiota*, as described by Hornibrook, can be readily distinguished from the holotype of *P. wilcoxensis* Cushman & Ponton (1932, pl. 8, figs 11a–b) by its distinctly asymmetrical test, more inflated chambers and higher and slightly asymmetrical aperture. The present material agrees well with the original description of the species. Specimens similar to that figured by Hornibrook (1958*b*, fig. 26) showing a wide open aperture were not observed in this material.

The derivation of *P. pseudoiota* from a globorotaliid ancestor has been suggested by earlier workers.

Distribution. This species was originally described from the Waipawan stage of New Zealand which Hornibrook dated as Palaeocene. He observed that it ranged up into the overlying Mangaorapan stage (Lower Eocene). It has been recorded from the Upper Palaeocene of Victoria, Australia (McGowran 1968).

In the Rakhi Nala section *P. pseudoiota* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis/Globorotalia esnaensis* Zones.

Pseudohastigerina sharkriverensis Berggren & Olsson

(Pl. 7, figs 1–2, 5–6)

1967 *Pseudohastigerina sharkriverensis* Berggren & Olsson: 280–281, pl. 1, figs 7–11; text-figs 7–8.

Remarks. The size and the shape of the test, the rate of enlargement and the inflation of the chambers, and the character of the aperture show variation in the present material.

The last two chambers sometimes make up more than one-half of the test as in the type material. Specimens with bipartite apertures (figs 1–2) were also observed. A weakly developed narrow lip usually borders the aperture.

P. sharkriverensis is readily distinguished from related contemporary species by its 5 to 6 inflated globular chambers in the last whorl, the last 2 to 3 of which enlarge much more rapidly in size than the earlier ones. Its globular chambers indicate a relationship with *P. pseudoiota* (Hornibrook) from which it seems to have been derived.

Distribution. *Pseudohastigerina sharkriverensis* was originally described from the early Middle Eocene of New Jersey, U.S.A.

In the Rakhi Nala section it occurs in the *Globorotalia crassata/Truncorotaloides topilensis* and *Truncorotaloides rohri* Zones.

Pseudohastigerina aff. wilcoxensis (Cushman & Ponton)

(Pl. 7, figs 9–10)

?1932 *Nonion wilcoxensis* Cushman & Ponton: 64, pl. 8, figs 11a–b.
1964 *Globanomalina ovalis* Haque; Loeblich & Tappan: c 665, fig. 531, 5a, b.

Remarks. The present form is characterized by a slightly evolute biumbilicate test; ovate equatorial periphery, subrounded axial periphery; about 5½ to 7 ovate, rapidly enlarging chambers in the last whorl; slightly curved, depressed sutures; smooth surface and low equatorial aperture provided with narrow lip. It is distinguished from *P. pseudoiota* (Hornibrook), with which it occurs associated in the material, by its evolute test, compressed chambers and lower, more symmetrical aperture.

With its compressed chambers and low symmetrical aperture the Pakistani form shows affinity to *P. wilcoxensis* Cushman & Ponton. However, the former differs in having a slightly evolute, less tightly coiled test and more chambers in the last whorl.

Pseudohastigerina eocenica (Berggren), described from the Lower Eocene of Denmark and Germany, shows a close resemblance to the present form in having a slightly evolute test and an equal number of chambers in the last whorl. Berggren's form, however, differs in having more inflated chambers.

The specimen from the Lower Eocene of Pakistan identified by Loeblich & Tappan (1964) as *Globanomalina ovalis* Haque, resembles the Rakhi Nala specimens in having a slightly evolute test, about 6 slightly compressed chambers, and a low equatorial aperture.

Distribution. *P.* aff. *wilcoxensis* occurs in the *Globorotalia formosa formosa* and *Globorotalia aspensis/Globorotalia esnaensis* Zones.

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PLATE 1

All figures approximately × 100 except 13–15, which are approximately × 50.

Figs. 1–3. ***Globigerina angustiumbilicata*** Bolli. P48827. Dorsal, peripheral and ventral views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 4–6. ***Globigerina praebulloides leroyi*** Blow & Banner. P48828. Ventral, peripheral and dorsal views. Sample 3658. ***Globigerina officinalis*** Zone, upper Khirthar Formation.

Figs 7–9. ***Globigerina officinalis*** Subbotina. P48829. Peripheral, ventral and dorsal views. Sample 3650, ***Globigerina officinalis*** Zone, upper Khirthar Formation.

Figs 10–12. ***Globigerina prolata*** Bolli. P48830. Dorsal, peripheral and ventral views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

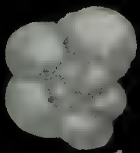
Figs 13–15. ***Globigerina posttriloculinoides clinata*** Khalilov. P48831. Peripheral, dorsal and ventral views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 16–18. ***Globigerina praebulloides occlusa*** Blow & Banner. P48832. Ventral, peripheral and dorsal views. Sample 3650, ***Globigerina officinalis*** Zone, upper Khirthar Formation.

Figs 19–21. ***Globigerina ouachitaensis*** Howe & Wallace. P48833. Dorsal, peripheral and ventral views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 22–24. ***Globigerina frontosa*** Subbotina. P48834. Ventral, peripheral and dorsal views. Sample 3606, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

PLATE 1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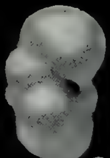
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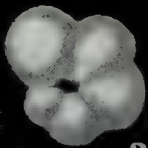
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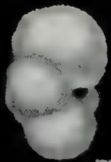
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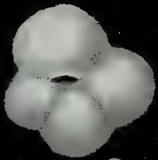
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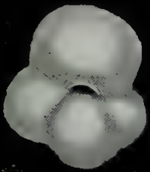
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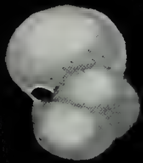
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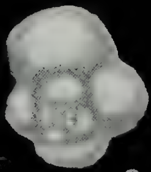
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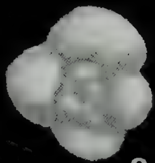
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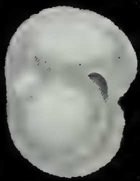
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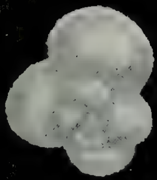
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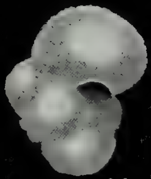
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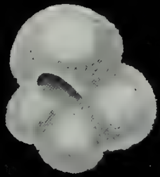
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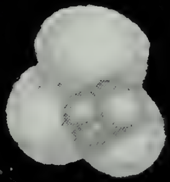
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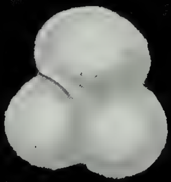
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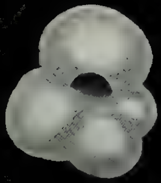
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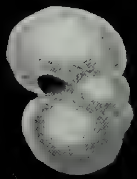
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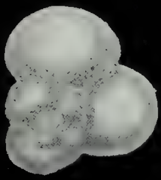
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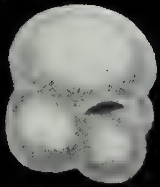
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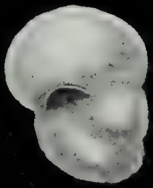
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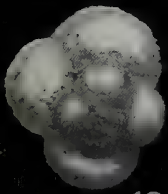
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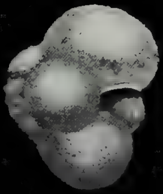
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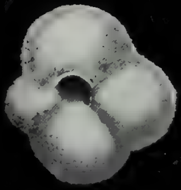
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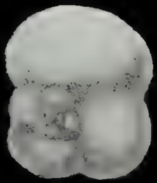
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PLATE 2

All figures approximately × 100.

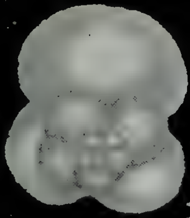
FIGS 1–3. **Globigerina azerbaidjanica** Khalilov. P48835. Dorsal, peripheral and ventral views. Sample 3650, **Globigerina officinalis** Zone, upper Khirthar Formation.

FIGS 4–6. **Globigerina baylissi** sp. nov. P48836. Dorsal, peripheral and ventral views. Holotype, sample 3622, **Truncorotaloides rohri** Zone, upper Khirthar Formation.

FIGS 7–9. **Globigerina inaequispira** Subbotina. P48837. Dorsal, peripheral and ventral views. Sample 3613, **Truncorotaloides rohri** Zone, upper Khirthar Formation.

FIGS 10–12. **Globigerina ciperoensis** Bolli. P48838. Ventral, dorsal and peripheral views. Sample 3604, **Globorotalia crassata/Truncorotatoides topilensis** Zone, upper Khirthar Formation.

FIGS 13–15. **Globigerina triangularis** White. P48839. Dorsal, peripheral and ventral views. Sample 3670, **Globorotalia formosa formosa** Zone, upper Dunghan Formation.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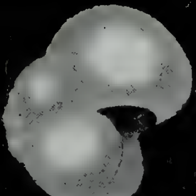
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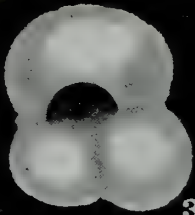
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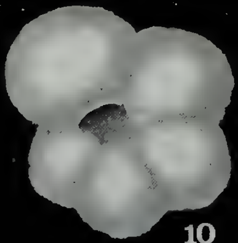
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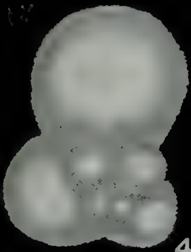
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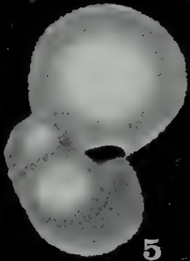
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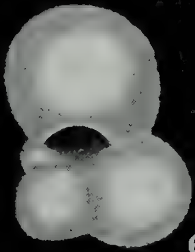
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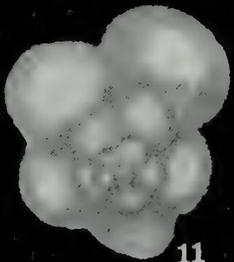
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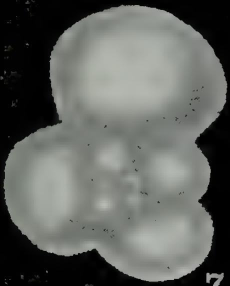
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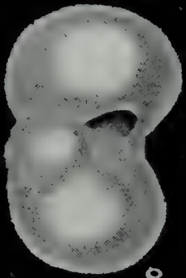
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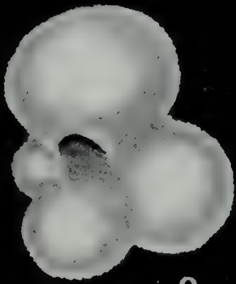
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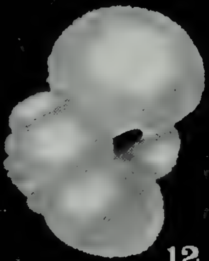
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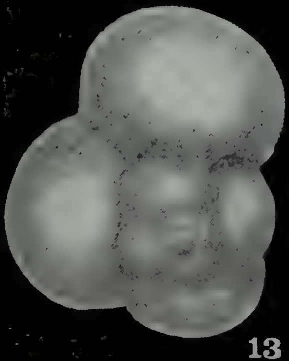
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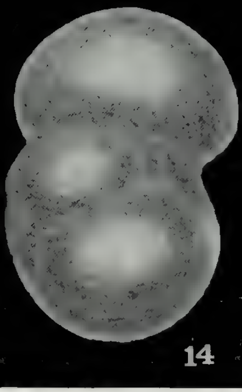
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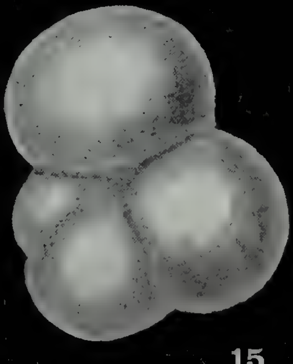
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PLATE 3

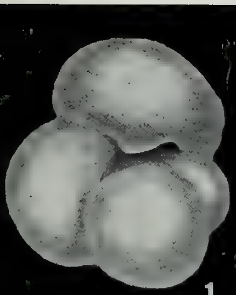
All figures approximately × 100 except 1–3, which are approximately × 50.

FIGS 1–3. ***Globigerina yeguaensis*** Weinzierl & Applin. P48840. Ventral, peripheral and dorsal views. Sample 3604, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIGS 4–6. ***Globigerina turgida*** Finlay. P48841. Dorsal, peripheral and ventral views. Sample 3670, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 7–9. ***Globigerina alanwoodi*** El-Naggar. P48842. Ventral, peripheral and dorsal views. Sample 3670, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 10–12. ***Globigerina velascoensis*** Cushman. P48843. Ventral, peripheral and dorsal views. Sample 3135, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.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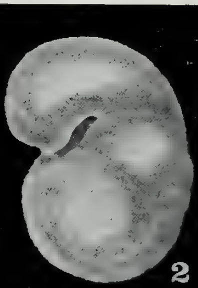
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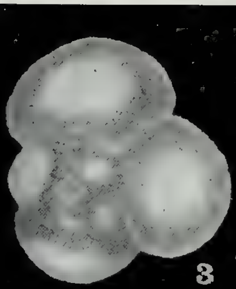
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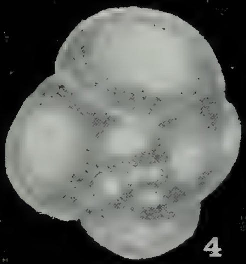
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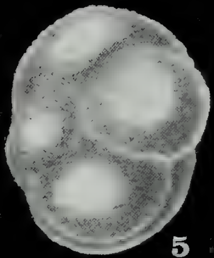
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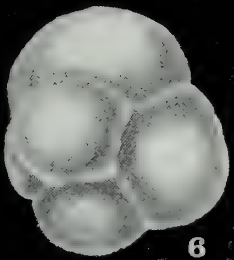
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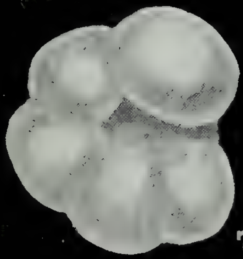
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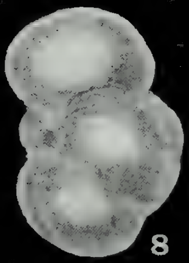
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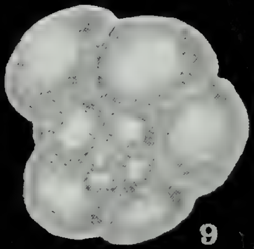
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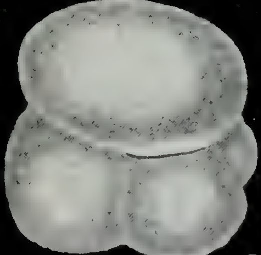
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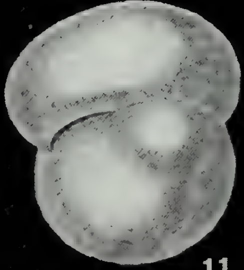
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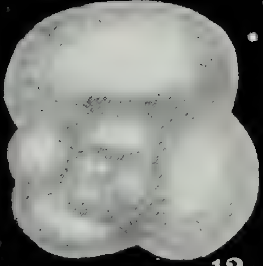
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PLATE 4

All figures approximately × 100.

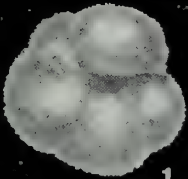
FIGS 1–3. ***Globigerina aquiensis*** Loeblich & Tappan. P48844. Ventral, peripheral and dorsal views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 4–6. ***Globigerina nodosa*** El-Naggar. P48845. Dorsal, peripheral and ventral views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 7–9. ***Globigerina haynesi*** El-Naggar. P48846. Dorsal, peripheral and ventral views. Sample 3135, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 10–12. ***Globigerina soldadoensis*** Bronnimann. P48847. Dorsal, ventral and peripheral views. Sample 3155, ***Globorotalia aspensis/Globorotalia esnaensis*** Zone, Ghazij Formation.

FIGS 13–15. ***Globigerina mckannai*** White. P48848. Dorsal, peripheral and ventral views. Sample 3670, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.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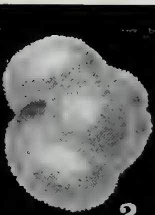
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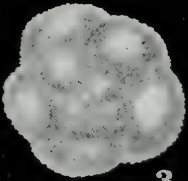
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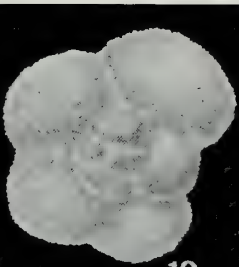
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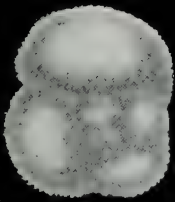
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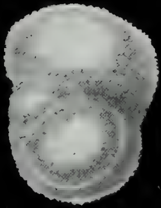
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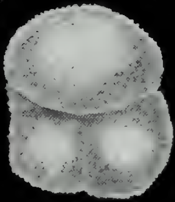
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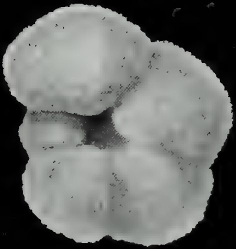
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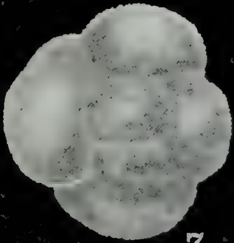
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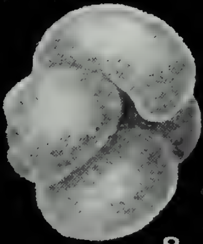
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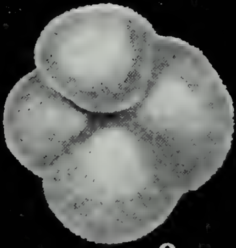
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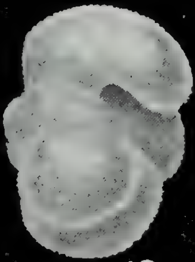
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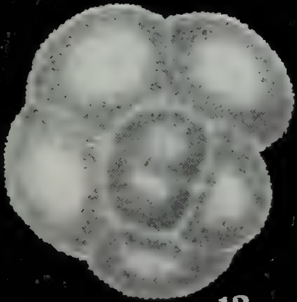
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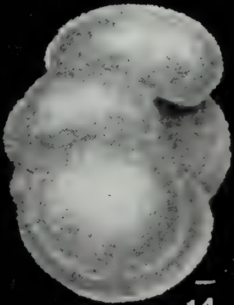
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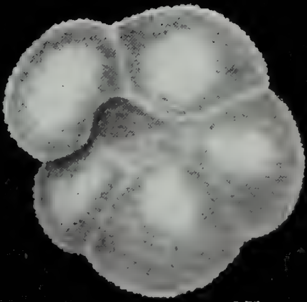
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PLATE 5

All figures approximately × 100.

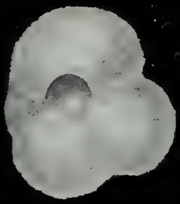
FIGS 1–3. ***Globigerinoides higginsi*** Bolli. P48849. Ventral, peripheral and dorsal views. Sample 3605, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIGS 4–6. ***Globigerinita echinita*** (Bolli). P48850. Ventral, peripheral and dorsal views. Sample 3605, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIGS 7–9. ***Globigerinita africana*** Blow & Banner. P48851. Dorsal, peripheral and ventral views. Sample 3608, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIGS 10–12. ***Globigerinita dissimilis*** (Cushman & Bermudez). P48852. Dorsal, peripheral and ventral views. Sample 3651, ***Globigerina officinalis*** Zone, upper Khirthar Formation.

FIGS 13–15. ***Globigerinita howei*** Blow & Banner. P48853. Dorsal, peripheral and ventral views. Sample 3604, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.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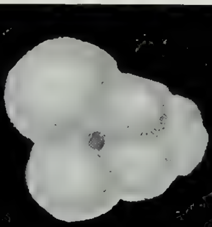
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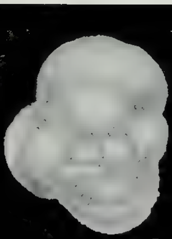
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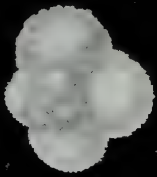
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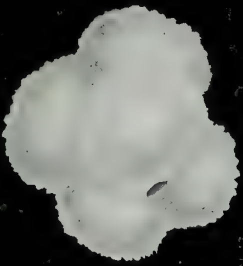
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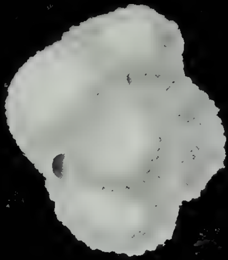
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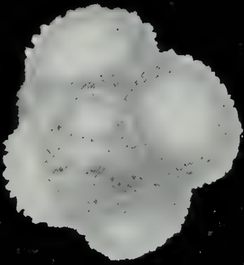
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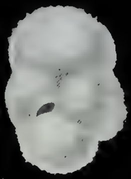
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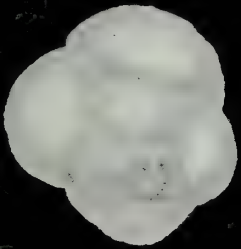
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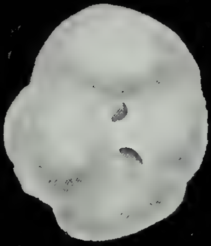
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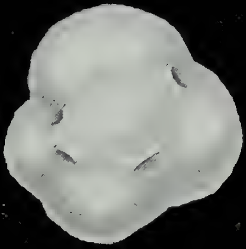
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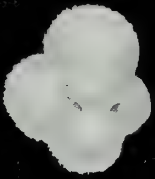
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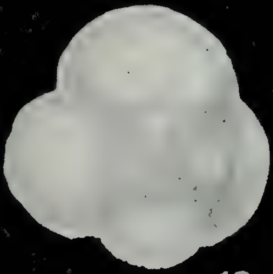
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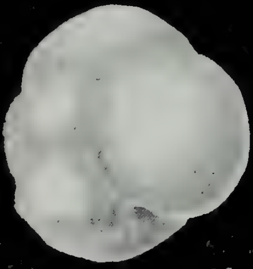
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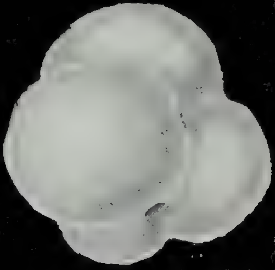
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PLATE 6

All figures approximately × 100.

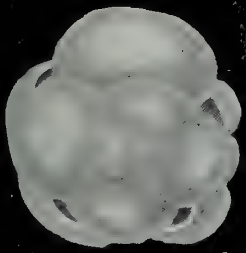
Figs 1–3. ***Globigerinatheka barri*** Bronnimann. P48854. Dorsal, peripheral and ventra views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, Upper Khirthar Formation.

Figs 4–6. ***Globigerapsis kugleri*** Bolli, Loeblich & Tappan. P48855. Ventral, peripheral and dorsal views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 7 & 8. ***Globigerapsis tropicalis*** Blow & Banner. P48856. Peripheral and dorsal views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 9 & 10. ***Truncorotaloides topilensis*** (Cushman). P48857. Dorsal and ventral views. Sample 3603, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 11 & 12. ***Truncorotaloides rohri*** Bronnimann & Bermudez. P48858. Ventral and dorsal views. Sample 3605. ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.



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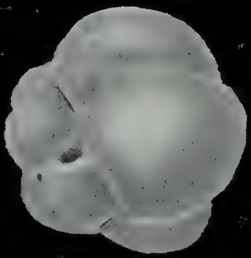

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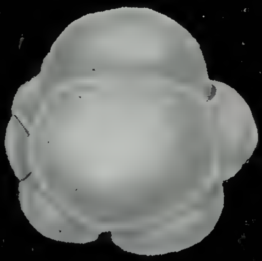

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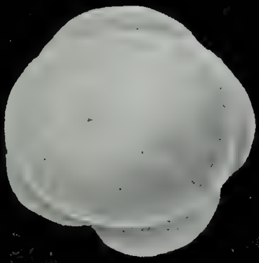

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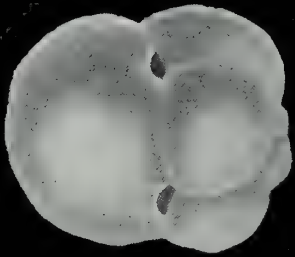

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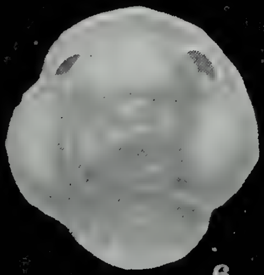

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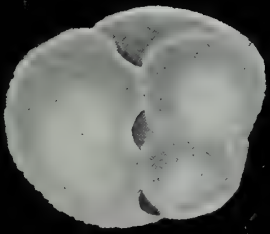

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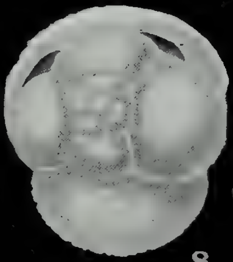

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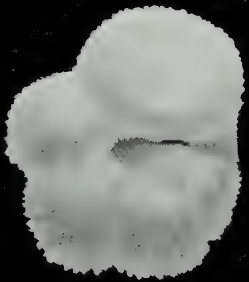

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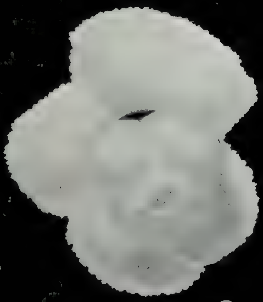

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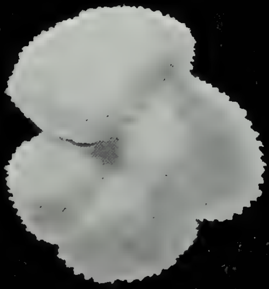

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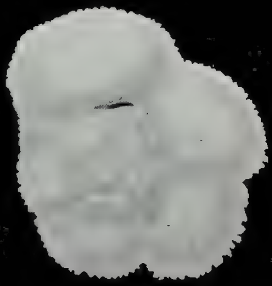

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PLATE 7

All figures approximately × 100.

FIGS 1 & 2, 5 & 6. ***Pseudohastigerina sharkriverensis*** Berggren & Olsson. 1, 5, peripheral views; 2, 6, side views. Figs 1 & 2, P48859. Sample 3624, ***Truncorotaloides rohri*** Zone; figs 5 & 6, P48861. Sample 3606, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone. Both upper Khirthar Formation.

FIGS 3 & 4. ***Pseudohastigerina pseudoiota*** (Hornibrook). P48860. Peripheral and side views. Sample 3672, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 7 & 8. ***Pseudohastigerina danvillensis*** (Howe & Wallace). P48862. Peripheral and side views. Sample 3622, ***Truncorotaloides rohri*** Zone, upper Khirthar Formation.

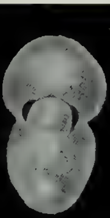
FIGS 9 & 10. ***Pseudohastigerina*** sp. aff. ***P. wilcoxensis*** (Cushman & Ponton.) P48863. Side and peripheral views. Sample 3672, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 11 & 12. ***Pseudohastigerina micra*** (Cole). P48864. Peripheral and side views. Sample 3625, ***Truncorotaloides rohri*** Zone, upper Khirthar Formation.

FIGS 13–15. ***Truncorotaloides collactea*** (Finlay). P48865. Ventral, peripheral and dorsal views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIGS 16 & 17. ***Hantkenina mexicana*** Cushman. Side views. Fig. 16, P48866; fig. 17, P48946. Sample 3606, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

FIG. 18. ***Hantkenina dumblei*** Weinzierl & Applin. P48867. Side view. Sample 3606, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.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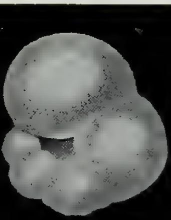
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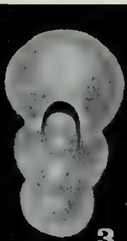
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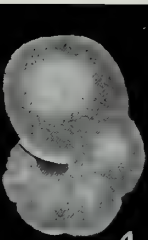
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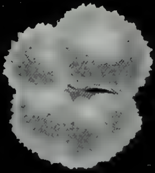
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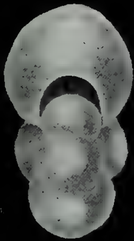
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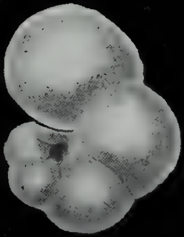
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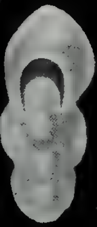
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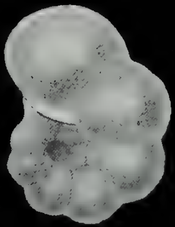
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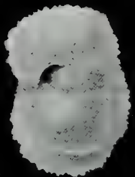
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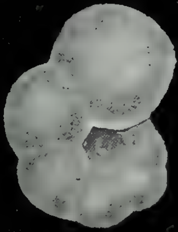
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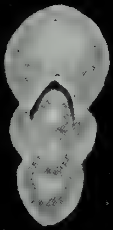
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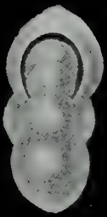
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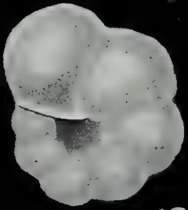
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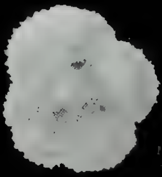
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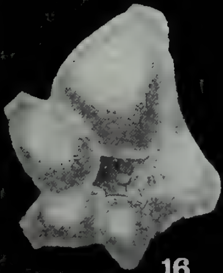
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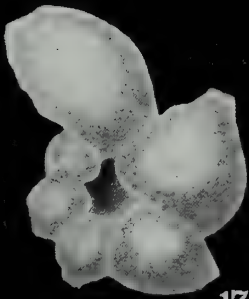
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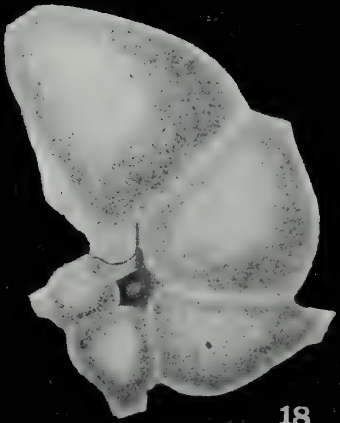
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PLATE 8

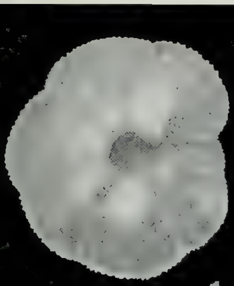
All figures approximately × 100.

FIGS 1–3. ***Globorotalia conicotruncata*** Subbotina. P48868. Ventral, peripheral and dorsal views. Sample 3133, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 4–6. ***Globorotalia aragonensis*** Nuttall. P48869. Ventral, peripheral and dorsal views. Sample 3140, ***Globorotalia aspensis*/*Globorotalia esnaensis*** Zone, Ghazij Formation.

FIGS 7–9. ***Globorotalia angulata*** (White). P48870. Ventral, peripheral and dorsal views. Sample 3130, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 10–12. ***Globorotalia tadjikistanensis*** Bykova. P48871. Dorsal, peripheral and ventral views. Sample 3135. ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.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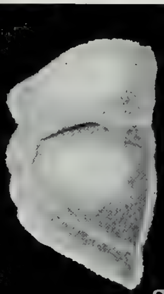
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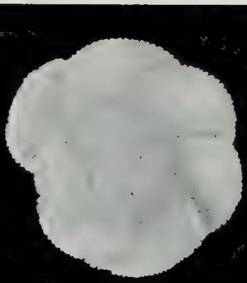
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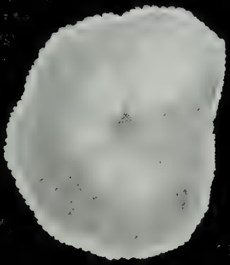
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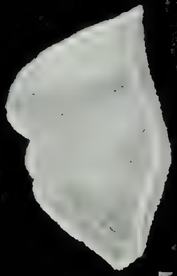
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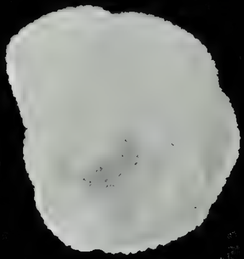
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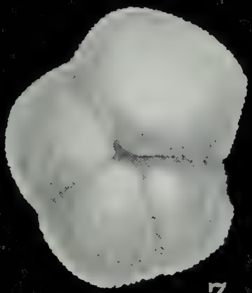
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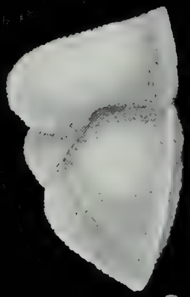
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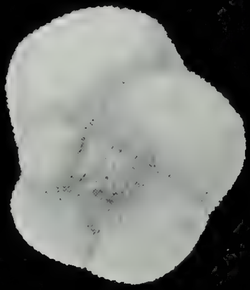
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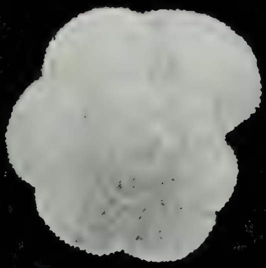
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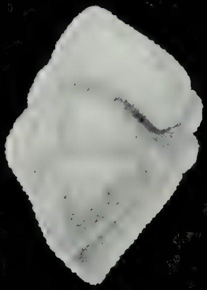
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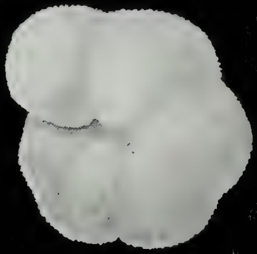
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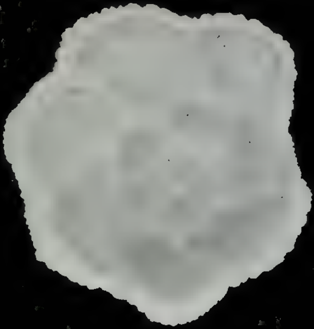
PLATE 9

All figures approximately × 100.

FIGS 1–3. ***Globorotalia formosa formosa*** Bolli. P48872. Dorsal, peripheral and ventral views. Sample 3670, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 4–6. ***Globorotalia parva*** Rey. P48873. Ventral, peripheral and dorsal views. Sample 3135, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 7–9. ***Globorotalia velascoensis*** (Cushman). P48874. Ventral, peripheral and dorsal views. Sample 3135, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.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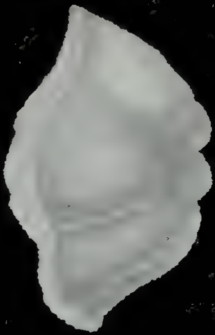
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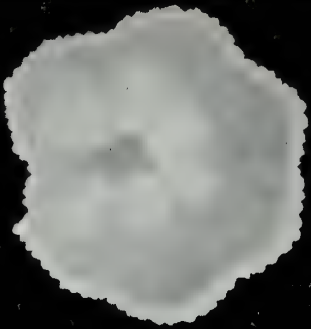
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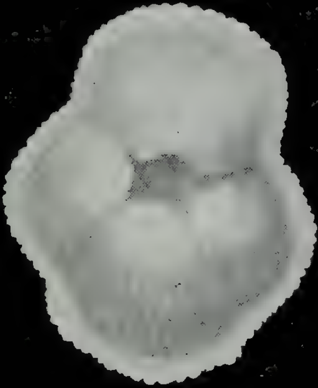
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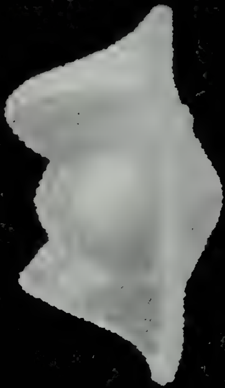
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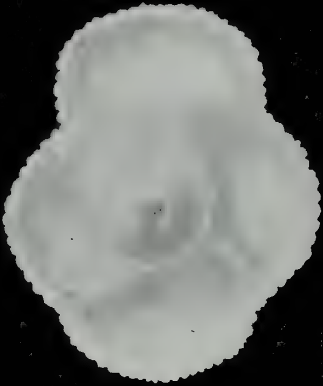
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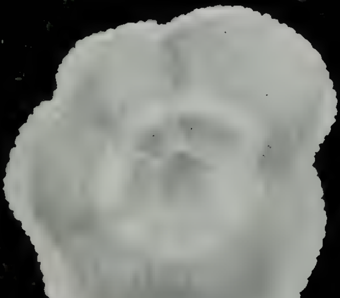
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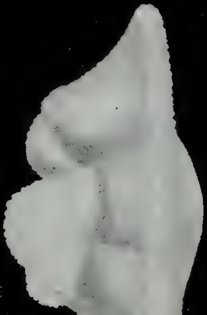
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PLATE 10

All figures approximately × 100.

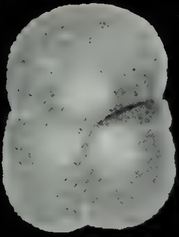
FIGS 1–4. ***Globorotalia aequa*** Cushman & Renz. Fig. 1, P48875. Ventral view; figs 2–4, P48876. Ventral, peripheral and dorsal views. Sample 3130, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 5–7. ***Globorotalia quetra*** Bolli. P48877. Dorsal, peripheral and ventral views. Sample 3672, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 8–10. ***Globorotalia acuta*** Toulmin. P48878. Ventral, peripheral and dorsal views. Sample 3130, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 11–13. ***Globorotalia occlusa*** Loeblich & Tappan. P48879. Ventral, peripheral and dorsal views. Sample 3131, ***Globorotalia velascoensis*** Zone, upper Dunghan Formation.

FIGS 14–16. ***Globorotalia subbotinae*** Morozova. P48880. Peripheral, ventral and dorsal views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.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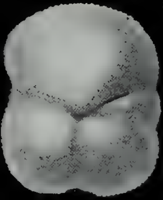
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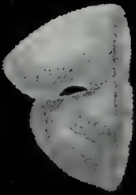
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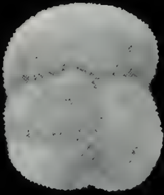
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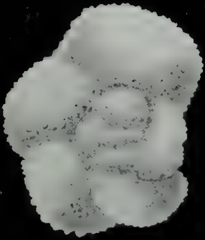
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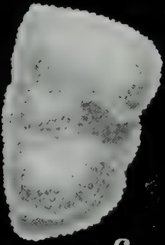
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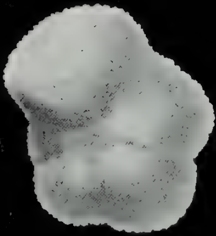
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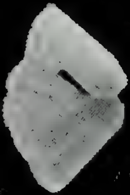
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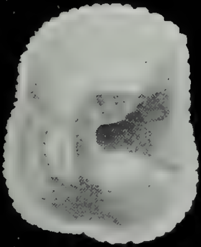
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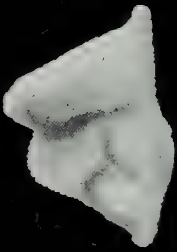
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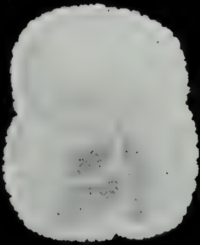
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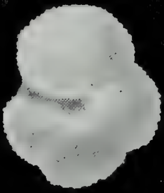
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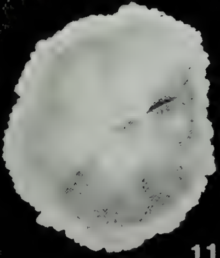
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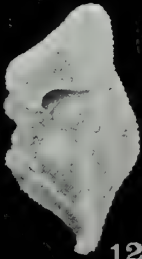
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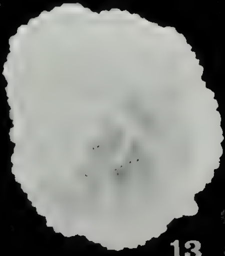
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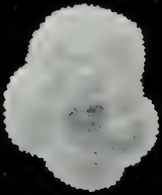
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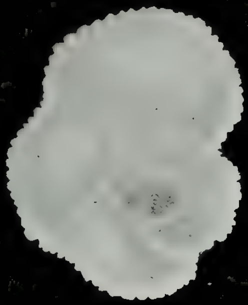
PLATE 11

All figures approximately × 100.

FIGS 1–3. ***Globorotalia marginodentata*** Subbotina. P48881. Dorsal, peripheral and ventral views. Sample 3138, ***Globorotalia aequa*** Zone, upper Dunghan Formation.

FIGS 4–6. ***Globorotalia formosa gracilis*** Bolli. P48882. Dorsal, peripheral and ventral views. Sample 3669, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

FIGS 7–9. ***Globorotalia crassata*** (Cushman). P48883. Dorsal, peripheral and ventral views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.



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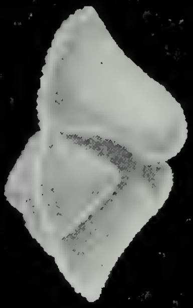

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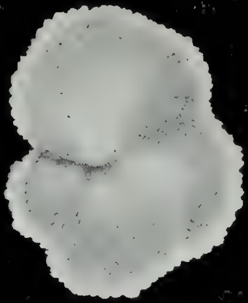

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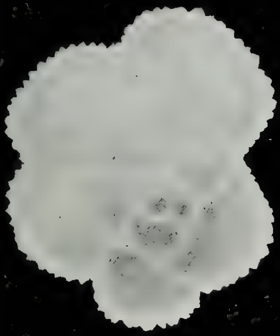

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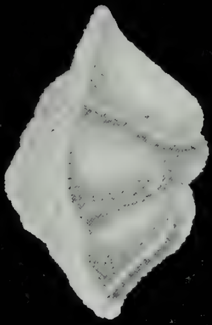

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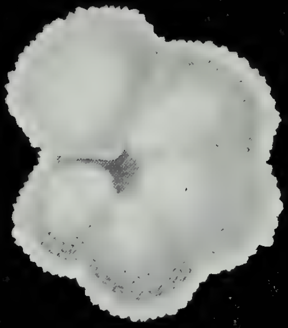

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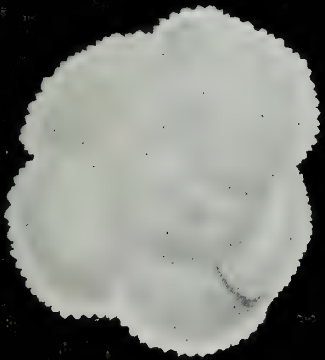

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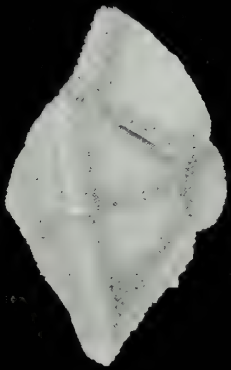

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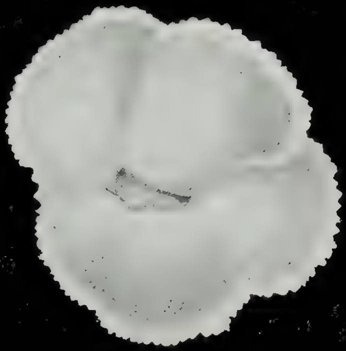

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PLATE 12

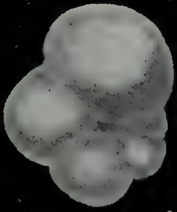
All figures approximately × 100.

Figs 1–3. ***Globorotalia pseudobulloides*** (Plummer). P48884. Ventral, peripheral and dorsal views. Sample 3135, ***Globorotalia velascoensis***, upper Dunghan Formation.

Figs 4–6. ***Globorotalia quadrata*** (White). P48885. Peripheral, ventral and dorsal views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

Figs 7–9. ***Globorotalia varianta*** (Subbotina) P48886. Peripheral, ventral and dorsal views. Sample 3140, ***Globorotalia aspensis*/*Globorotalia esnaensis*** Zone, Ghazij Formation.

Figs 10–12. ***Globorotalia centralis*** Cushman & Bermudez. P48887. Ventral, peripheral and dorsal views. Sample 3606, ***Globorotalia crassata*/*Truncorotaloides topilensis*** Zone, upper Khirthar Formation.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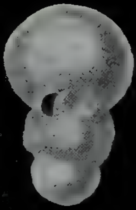
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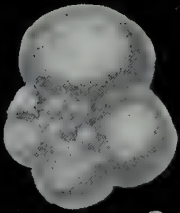
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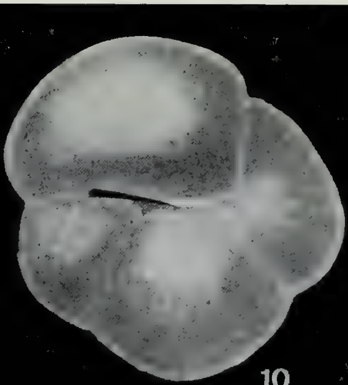
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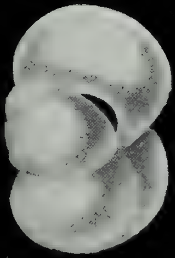
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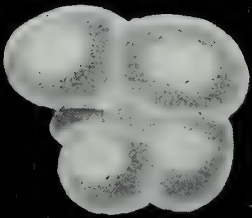
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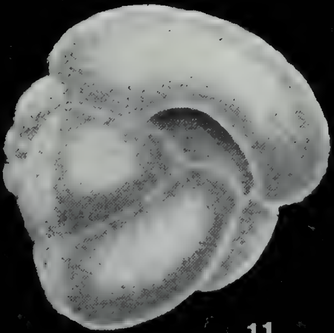
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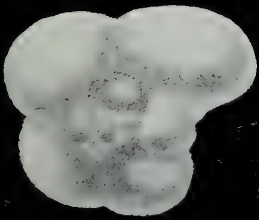
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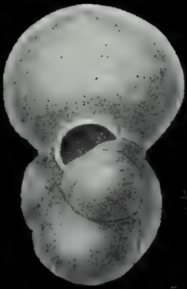
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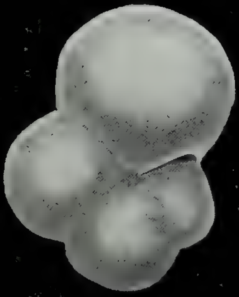
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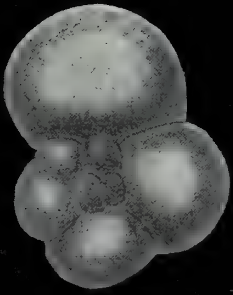
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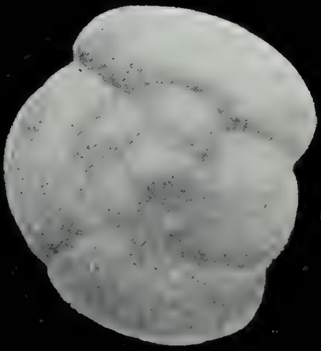
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PLATE 13

All figures approximately × 100.

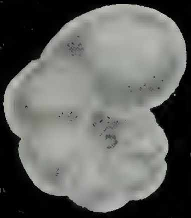
FIGS 1–3. **Globorotalia troelseni** Loeblich & Tappan. P48888. Dorsal, peripheral and ventral views. Sample 3137, **Globorotalia velascoensis** Zone, upper Dunghan Formation.

FIGS 4–6. **Globorotalia ehrenbergi** Bolli. P48889. Dorsal, peripheral and ventral views. Sample 3135, **Globorotalia velascoensis** Zone, upper Dunghan Formation.

FIGS 7–9. **Globorotalia pseudomenardii** Bolli. P48890. Ventral, peripheral and dorsal views. Sample 3135, **Globorotalia velascoensis** Zone, upper Dunghan Formation.

FIGS 10–12. **Globorotalia renzi** Bolli. P48891. Dorsal, ventral and peripheral views. Sample 3623, **Truncorotaloides rohri** Zone, upper Khirthar Formation.

FIGS 13–15. **Globorotalia chapmani** Parr. P48892. Dorsal, peripheral and ventral views. Sample 3135, **Globorotalia velascoensis** Zone, upper Dunghan Formation.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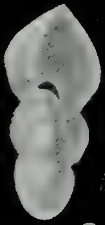
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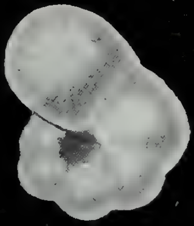
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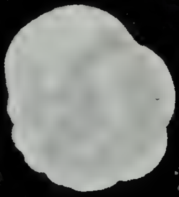
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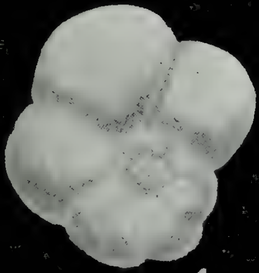
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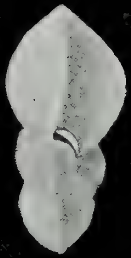
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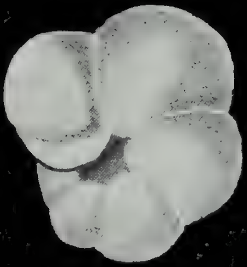
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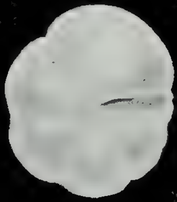
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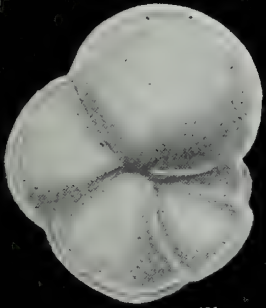
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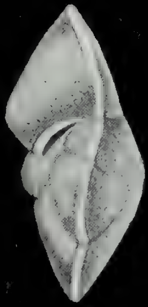
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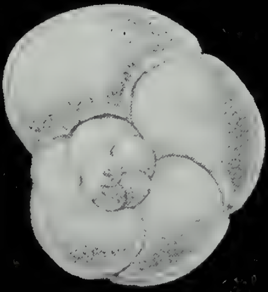
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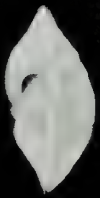
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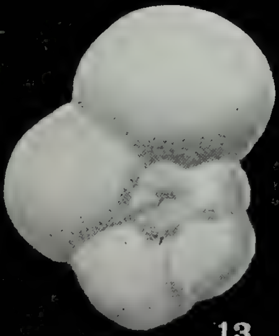
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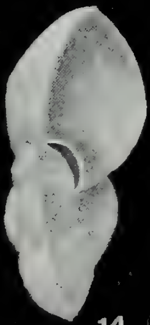
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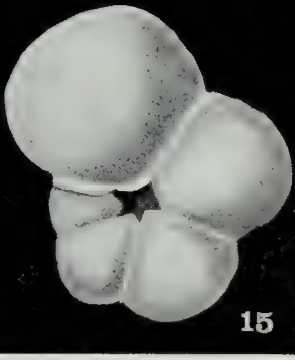
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PLATE 14

All figures approximately × 100.

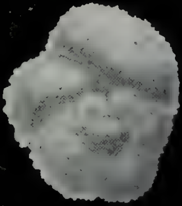
Figs 1–3. ***Globorotalia spinulosa*** Cushman. P48893. Dorsal, peripheral and ventral views. Sample 3605, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 4–6. ***Globorotalia irrorata*** Loeblich & Tappan. P48894. Dorsal, peripheral and ventral views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

Figs 7 & 8. ***Chiloguembelina goodwini*** (Cushman & Jarvis). P48895. Side and peripheral views. Sample 3622, ***Truncorotaloides rohri*** Zone, upper Khirthar Formation.

Figs 9–11. ***Globorotalia*** sp. aff. ***G. primitiva*** (Finlay). P48896. Ventral, peripheral and dorsal views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.

Figs 12–14. ***Globorotalia lehneri*** Cushman & Jarvis. P48897. Ventral, peripheral and dorsal views. Sample 3604, ***Globorotalia crassata/Truncorotaloides topilensis*** Zone, upper Khirthar Formation.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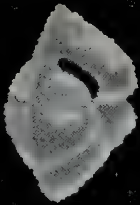
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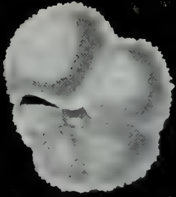
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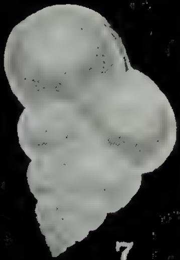
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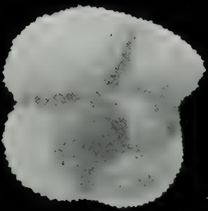
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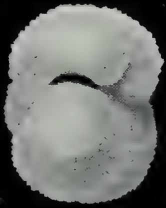
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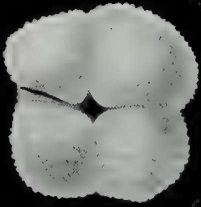
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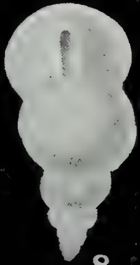
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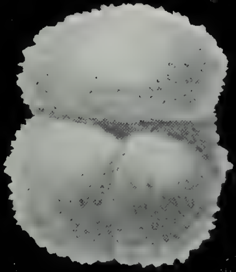
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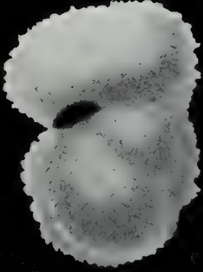
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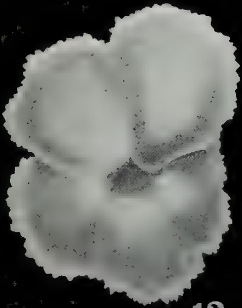
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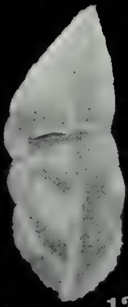
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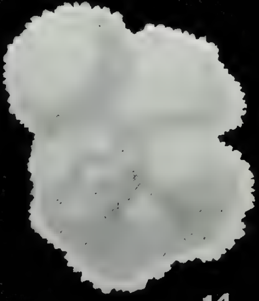
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PLATE 15

All figures approximately × 100.

Figs 1–3. ***Globorotalia whitei*** Weiss. P48898. Dorsal, peripheral and ventral views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

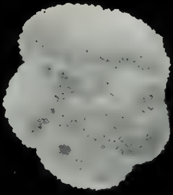
Figs 4–6. ***Globorotalia broedermanni*** Cushman & Bermudez. P48899. Ventral, peripheral and dorsal views. Sample 3140, ***Globorotalia aspensis/Globorotalia esnaensis*** Zone, Ghazij Formation.

Figs 7–9. ***Globorotalia esnaensis*** (Le Roy). P48900. Dorsal, peripheral and ventral views. Sample 3671, ***Globorotalia formosa formosa*** Zone, upper Dunghan Formation.

Figs 10–12. ***Globorotalia aspensis*** (Colom). P48901. Dorsal, peripheral and ventral views. Sample 3155, ***Globorotalia aspensis/Globorotalia esnaensis*** Zone, Ghazij Formation.

Figs 13 & 14. ***Chiloguembelina martini*** (Pijpers). P48902. Side and peripheral view. Sample 3621, ***Truncorotaloides rohri*** Zone, upper Khirthar Formation.

Figs 15 & 16. ***Chiloguembelina woodi*** sp. nov. P48903. Side and peripheral views. Holotype, sample 3622, ***Truncorotaloides rohri*** Zone, upper Khirthar Formation.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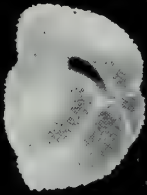
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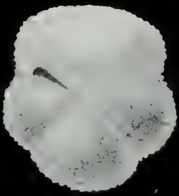
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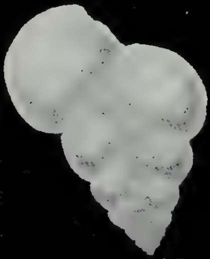
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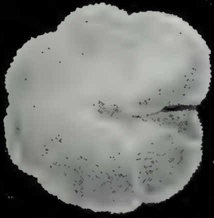
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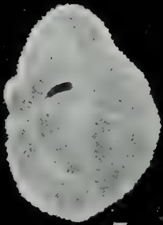
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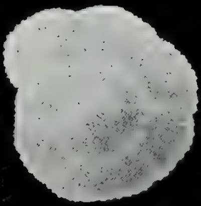
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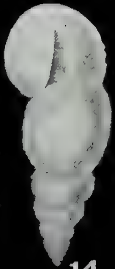
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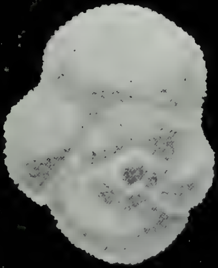
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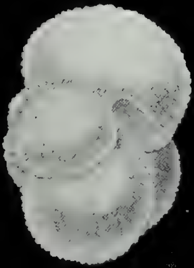
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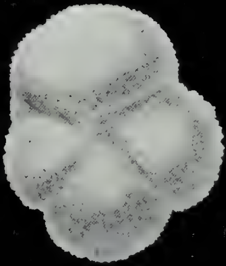
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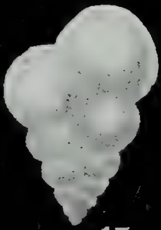
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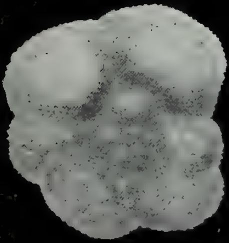
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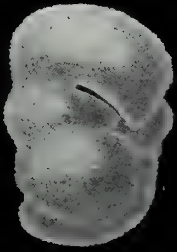
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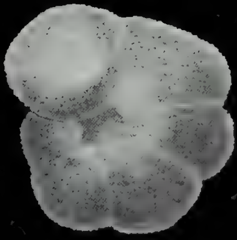
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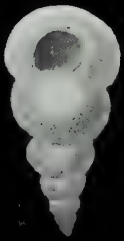
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MEGISTOTHERIUM, GIGANTIC HYAENODONT FROM MIOCENE OF GEBEL ZELTEN, LIBYA

R. J. G. SAVAGE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 22 No. 7
LONDON: 1973

MEGISTOTHERIUM, GIGANTIC HYAENODONT FROM MIOCENE OF GEBEL ZELTEN, LIBYA

28 MAR

BY

ROBERT J. G. SAVAGE

Department of Geology, University of Bristol

Pp. 483–511; 4 *Plates*, 20 *Text-figures*

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By R. J. G. SAVAGE

CONTENTS

I.	Introduction and acknowledgments	485
II.	Systematic description	485
	Family Hyaenodontidae Leidy 1869	486
	Subfamily Hyaenodontinae	486
	Genus *Megistotherium* gen. nov.	486
	Megistotherium osteothlastes gen. et sp. nov.	487
III.	Discussion	503
IV.	Other material referable to and comparable with *Megistotherium*	507
V.	References	511

SYNOPSIS

A description is given of *Megistotherium osteothlastes*, g. et sp. nov., based largely on a complete skull from Lower Miocene sediments of Gebel Zelten, Libya. The beast is the largest known carnivore: a functional analysis is given and fragments of comparable species from Eurasia and East Africa are discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

In the course of preliminary geological exploration around Gebel Zelten in 1962 and 1963, prospectors found bones among which were some that appeared to belong to a gigantic carnivore. During my first expedition to Gebel Zelten in 1964 I found several more post-cranial fragments that appeared to belong to a similarly large beast. In 1966 I discovered a complete skull of a gigantic hyaenodont, the subject of this paper. An account of the geological setting and the faunal assemblage of the Gebel Zelten area is given in the first paper in the series (Savage & Hamilton 1972). Others on each of the major groups in the mammalian fauna will follow.

It is a great privilege to acknowledge my very grateful thanks to Mr George L. de Coster, of Esso Standard Libya Inc., through whose generosity the magnificent skull is now in the collection of the British Museum (Natural History). I should also like to acknowledge the co-operation and facilities offered my parties in the field by Esso Standard and Oasis Oil Company. The field work has been supported by grants from the Leverhulme Foundation and the Natural Environments Research Council. I have profited from discussions on the brain with Dr L. B. Radinsky and on the ear region with Dr G. T. MacIntyre. I am indebted to Mr R. Godwin for the photography, to Mrs Joyce Treuherz for the drawings in Figs. 1–5, to Miss Mary Rampton for all the other drawings, and to my wife Shirley Coryndon for her patience, criticism and help at all times.

II. SYSTEMATIC DESCRIPTION

Family **HYAENODONTIDAE** Leidy 1869

Diagnosis. Creodonta with upper molars either three or reduced to two; two front upper molars specialized as carnassial teeth, either tuberculosectorial or completely sectorial; last upper molar, when present, transversely extended; all the lower molars specialized as carnassial teeth; P $\frac{1}{1}$ two-rooted, except in some specialized genera; primitive forms with long and slender skulls, tail long and heavy; later forms with robust skull, claws blunt; cursorial adaptations to a varying extent (Savage 1965).

Remarks. This is not the place to discuss the problems of higher taxonomic grouping. Within the Family Hyaenodontidae I place only the Proviverrinae and the Hyaenodontinae. I follow Gazin (1946) in separating the Limnocyoninae and the Machaeroidinae in a separate family the Limnocyontidae. The Teratodontidae (Savage 1965) seems best left as a separate family until more is known.

Subfamily **HYAENODONTINAE** Leidy 1869

Diagnosis. Hyaenodontidae with narrow skull and long face; M $\frac{3}{3}$ or M $\frac{2}{3}$; molars sectorial, length greater than width; M^3 small and transverse or absent; M^{1+2} with paracone and metacone completely or nearly connate, protocone reduced or absent; lower molars without metaconid, talonid vestigial or absent (Savage 1965).

Remarks. Van Valen (1966) used the term 'tribe Hyaenodontini' essentially as synonymous with my use (Savage 1965) of it at subfamily rank. Van Valen (1967) abandoned the use of tribes and lumped into his 'subfamily Hyaenodontinae' all Hyaenodontinae *sensu stricto*, Proviverrinae, Hyainailourinae and Teratodontidae; this makes a very unmanageable subfamily of 19 genera. The subfamily Hyaenodontinae as defined above and as used below, differs from Savage (1965) in essentially only one aspect, namely the inclusion of the now much better known Hyainailourinae. Basically the subfamily comprises the genera *Pterodon*, *Metapterodon*, *Hyaenodon*, *Leakitherium*, *Hyainailouros* and *Megistotherium*. Three further genera are of less certain affinity; *Apterodon* [=*Dasyurodon*], which was placed in a separate tribe of the subfamily by Szalay (1967); *Propterodon*, poorly known and placed in the tribe Proviverrini by Van Valen (1966); and *Ischnognathus*, again poorly known but compared by Patterson (in Stovall 1948) to *Hemipsalodon*, which is very similar to if not synonymous with *Pterodon*. The new material described below makes clear the inclusion of *Hyainailouros* in the subfamily.

Genus ***MEGISTOTHERIUM*** gen. nov.

Diagnosis. Gigantic hyaenodontine, dental formula $\frac{1\ 1\ 4\ 3}{?\,3\ 1\ 4\ 3}$; single large upper incisor, very large upper canine, laterally placed with respect to other teeth; palate very constricted around P^{1+2}; P^{3+4} three-rooted, P^4 width greater than length; M^{1+2} trenchant; M^3 small transverse. Jugal arch heavy and wide, sagittal crest high.

Type species. *M. osteothlastes* gen. et sp. nov.

Remarks. The completeness of the cranial material makes comparison with the poorly known *Hyainailouros* difficult, but the dentitions where comparable show sufficient differences for the new material to warrant generic distinction. The genus is larger than any other known hyaenodontid.

Megistotherium osteothlastes sp. nov.

(Text-figs 1–17; Plates I–IV)

DIAGNOSIS. As for genus. The generic name is derived from the Greek μεγιστος greatest and θηρός beast. The trivial name comes from οδτεος bone and θλαδτος crusher.

HOLOTYPE. M 26173. Collections of British Museum (Natural History). From the southeast corner of Gebel Zelten, Libya, at 28° North, 20° 30′ East. Early Miocene. Site 6412.

HYPODIGM. Holotype together with the following, all from Gebel Zelten.

Reg. No.	*Site*	
M 26515	6424	Cranium
M 26516	,,	Premaxillae with root of left incisor
M 26517	,,	Left maxilla fragment with root/alveoli of M^{1-3}
M 26518	,,	Right maxilla fragment with roots/alveoli of M^{1-3}
M 21902	,,	Atlas
UB 20576	6412	Distal end of right humerus
UB 20577	6405	Distal end of right humerus
UB 20578	6412	Left magnum
UB 20579	6412	Right astragalus
UB 20580	6412	Metapodial
UB 20581	6416	Metapodial
UB 20582	6416	Metapodial
UB 20583	6424	Metapodial

Four specimens in the British Museum collections (M 26515–26518) are associated fragments of a second skull. These were collected by oil prospectors and the exact location is unrecorded. The second skull is slightly smaller than the type and by the presence of open sutures patently that of a younger individual. Item M 26515 comprises the braincase and the description below of the brain and sinuses is based very largely on this specimen. Registered numbers with the prefix UB refer to the collections in the Geology Museum, University of Bristol.

DESCRIPTION. The most striking feature of this impressive skull is its size; the overall length is 66·4 cm. and span across the jugal arches is 47·1 cm. The skull possesses the largest sagittal crest known and enormous canines. The whole structure of the skull is extremely massive and robust; the bones are well fused. Although the crowns of the teeth are in most cases lacking, those that survive do not suggest that the individual was very old. There are several areas of bone disease which could have been the cause of death.

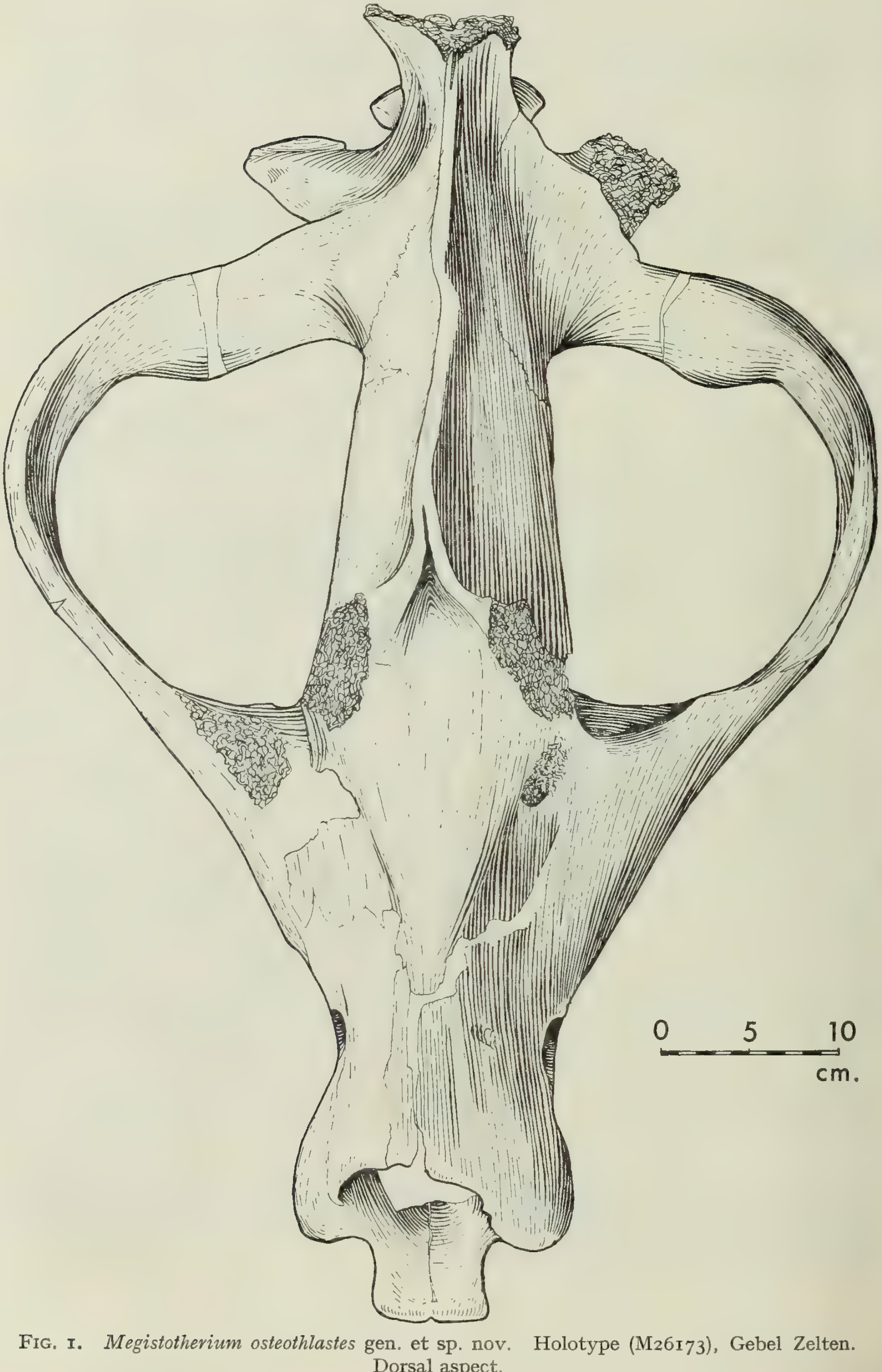


FIG. 1. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Dorsal aspect.

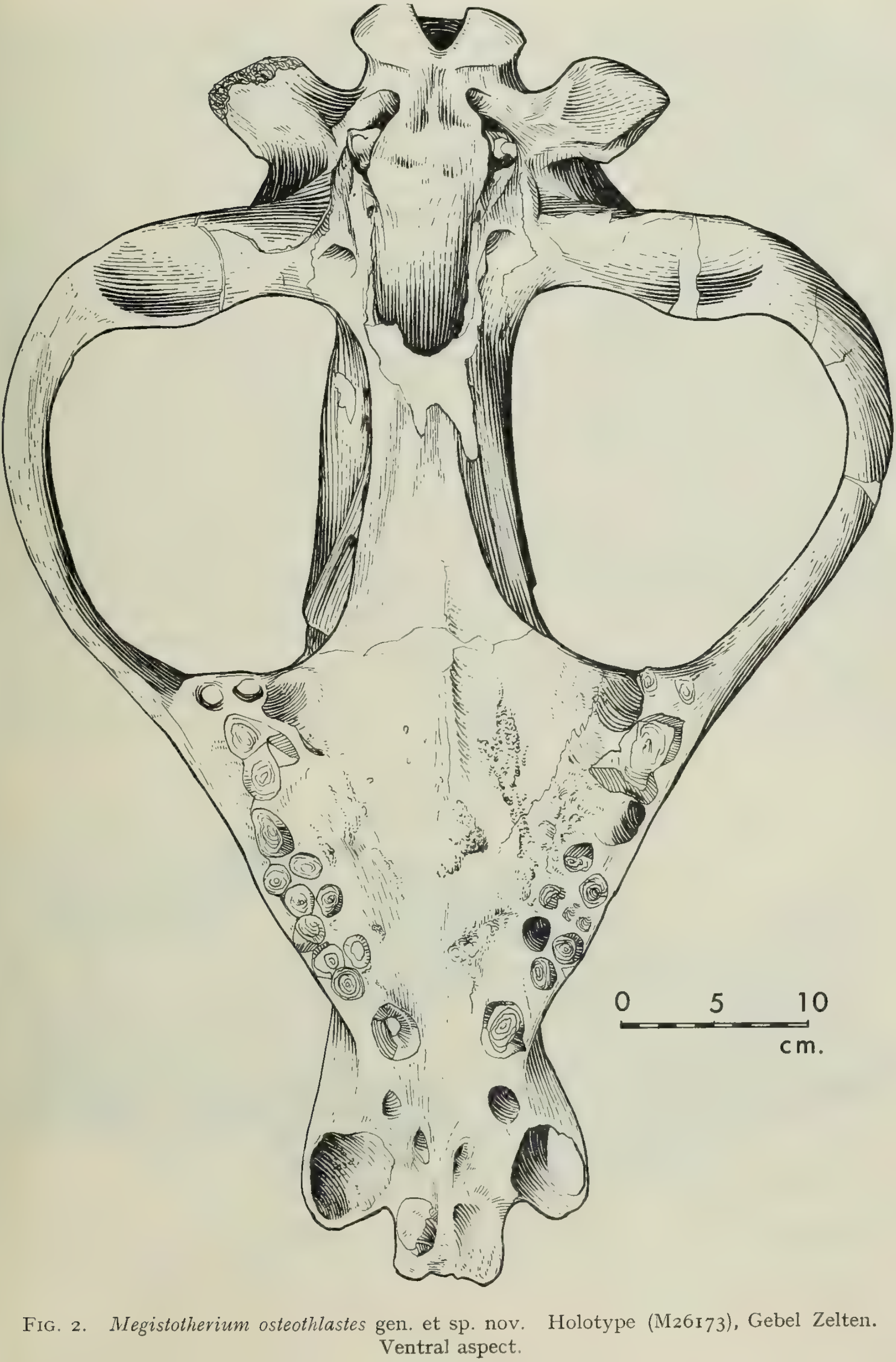


FIG. 2. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Ventral aspect.

No attempt is made to give an exhaustive account of every bone in the skull. The aim is rather to point to the salient features which characterize the animal and lead to a functional understanding.

Premaxilla. Although the limits of the bone cannot be defined, the major function is to carry the single large pair of incisors. The premaxillae stand well proud of the canines; between the anteriorly placed premaxilla and the laterally placed canine behind, is a deep groove for the accommodation of the lower canine.

Maxilla. The anterior margin of the maxilla is greatly expanded laterally to house the large upper canine; the canine alveolus and infra-orbital foramen are about the same size. The palate is V-shaped, extremely narrow at the level of P^1 and very wide posteriorly opposite M^3. The palatine fossae are close together between the canines and numerous nutrient foramina perforate the palate. A series of large deep and highly vascularised embrasure pits is developed on the palate between the protocones of the molars and premolars, reminiscent of the condition seen in the larger mesonychids.

Nasal. The right nasal is broken but on the left side the bone appears to extend back as far as the postorbital process of the frontal. The anterior narial opening is wide and high.

Lacrymal. Wanting on the right side, while on the left the area around the foramen is poorly preserved.

Jugal. On both sides the bone is well preserved, due in no small measure to its robust build; the bone carries a prominent infraorbital tubercle. Posteroventrally the ramus extends almost as far as the glenoid articulation of the squamosal.

Palatine. The anterior suture between the maxilla and the palatine can be partially traced; much of the very wide palate posterior to M^1 is roofed by palatine bone; this narrows dramatically behind the last molar and extends posteriorly

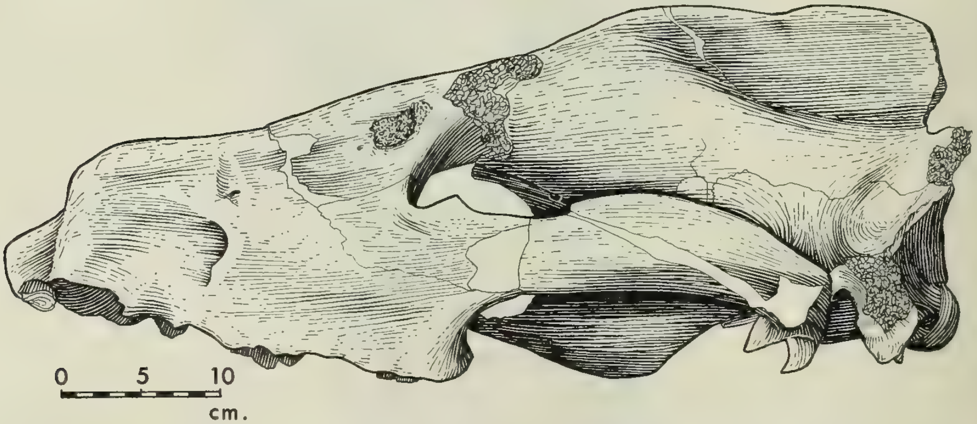


FIG. 3. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Lateral aspect.

almost to the level of the glenoid articulation. The posterior margin is broken, but even allowing for this it is clear that the hard palate extends posteriorly considerably further than in other hyaenodonts. The posterior narial opening is 5 cm in diameter, similar in area to the anterior nares. There is a median longitudinal ridge along the ventral length of the palatine; the absence of the lateral walls suggests a thinning of the bone in this region.

Vomer. This bone cannot be seen in the specimen.

Frontal. In the absence of sutures the limits of the frontals cannot be drawn. In transverse section across the frontals the skull has the form of two cylinders; the lower and smaller one for the narial passage, and the upper formed of frontal bone which is extended dorsally to form the anterior part of the sagittal crest. Though broken, there appears to have been a massive postorbital frontal process. From near each postorbital process a ridge arises, increasing in height posteromedially until the two meet in the midline; they then continue posteriorly as a great plate of bone, the sagittal crest. The consequent V-shaped pit left anterior to the crest is reminiscent of some bats and bears witness to the origin of the crest by the upfolding of a pair of ridges.

Parietal. Even though the sutures are not open, it is clear that this bone contributes very largely to the formation of the sagittal crest. The crest is 30 cm long and some 15 cm deep. This depth is attained not so much by raising the crest as by the comparatively minute braincase which enables the crest to descend much lower than would be the case in a true carnivore. The crest is flared out postero-

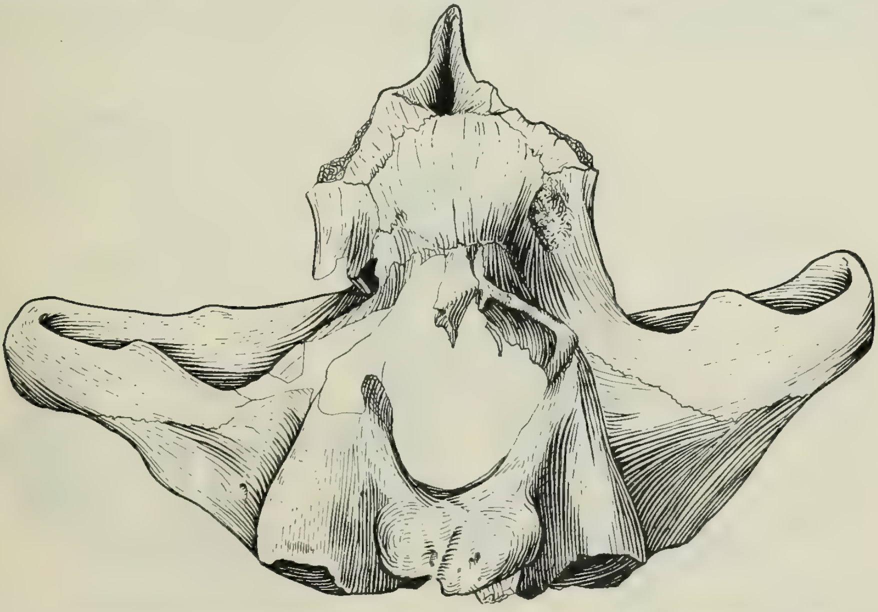


FIG. 4. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Anterior aspect.

laterally against the supraoccipital. Although the crest forms a vertical plate of bone, it is not quite flat; the distinct kinks could reflect slight differences in development of temporal muscle on left and right sides, or may be due to postmortem changes—the skull was fossilized with the dorsal surface facing downwards. The crest carries on the right side a large nutrient foramen.

Occipital. Viewed posteriorly the skull presents a trefoil pattern, formed of supraoccipital and two exoccipitals. The supraoccipital, broken dorsally, is sphenoidal, narrowing toward the foramen magnum. A pair of very large pits occupying most of the supraoccipitals witness the enormous rectus capitis musculature. Immediately below these are two very large nutrient foramina which pass ventrally to a common opening on the roof of the foramen magnum. The exoccipital is dominated by the wide and massive paraccipital process; no separate mastoid process can be distinguished. The heavy paroccipitals must have carried heavy rectus capitis anterior and lateralis muscles for lateral head movements. The foramen magnum is roughly circular in outline and about 3·5 cm in diameter; on its inner margin it carries dorsally an opening which communicates with the two nutrient foramina on the supraoccipital. On the internolateral border can be seen the posterior lacerate foramen which passes anteriorly to open in the ear region. On the ventrolateral border is a further opening from the foramen magnum to the basioccipital, with a passage leading toward the ear region. The occipital condyles are large ovoidal facets, strongly keeled, with long axis directed ventromedially; the condyles almost meet ventrally with only a shallow notch separating them. The basioccipital is a relatively thin bridge of bone between the exoccipitals and the massive basisphenoid; the paired anterior condyloid foramen is clearly visible.

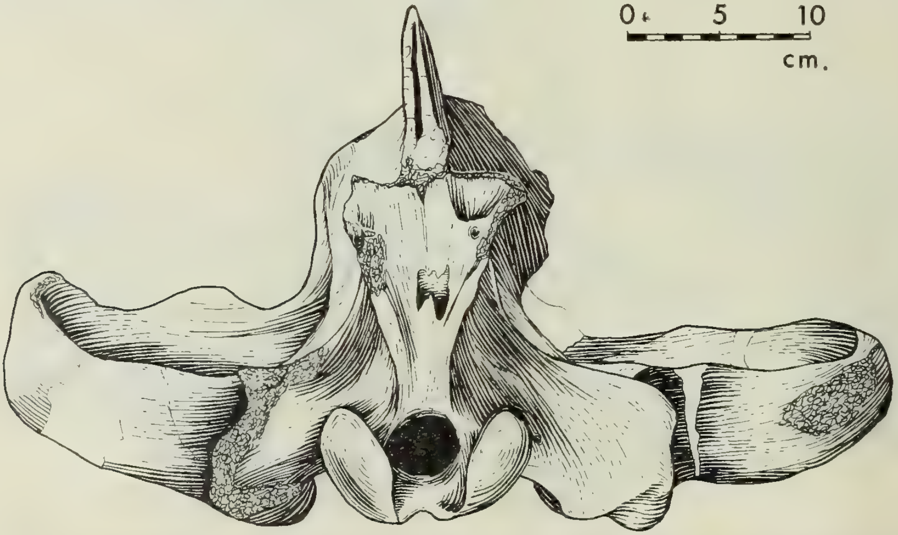


FIG. 5. *Megistotherium osteothlastes* gen. et sp. nov. Holotype (M26173), Gebel Zelten. Posterior aspect.

Ethmoid. This bone is not preserved in the fossil.

Sphenoid. The orbitosphenoid is lacking, the presphenoid is not visible and probably not preserved. The basisphenoid is massively built and literally deserves its name by forming a solid wedge between the squasomal glenoid articulations: without this the jaw joint would lack rigidity, powerful muscle action become impossible and there would be risk of crushing in the ear region and damage to the brain. The ventral surface of the basisphenoid carries a transverse ridge, which would have added strength to the bone and may have also served for the attachment of anterior strands of the rectus capitis anticus musculature: on the dorsal surface the sella turcica is shallow and poorly defined. Most of the alisphenoid is present; although the tips of the pterygoid processes are missing these appear to have been of normal proportions. The alisphenoid is pierced by a series of five openings for the cranial nerves and these have been identified as shown in Fig. 6. The separation of the foramen rotundum and the foramen lacerum anticum points to the uncrowded condition in this region, rarely seen in other creodonts. As in *Hyaenodon* there is no alisphenoid canal and the carotid artery lay in a shallow groove alongside the alar process.

Squamosal. The ·bone is dominated by the massive glenoid articulation for the mandible. The glenoid is deep, concave and with a length of 13 cm; it is buttressed by stout processes anterolaterally and posteromedially. A stout ridge extends on the dorsal surface from the glenoid area, posteromedially above the paraccipitol process, strengthening the bone to resist mandibular forces. The suture of the squamosal with the parietal remains open anteriorly. As mentioned above, no separate mastoid process is dinstinguishable and it is presumably fused with the paroccipital process. A long deep trench, extending laterally and horizontally between the

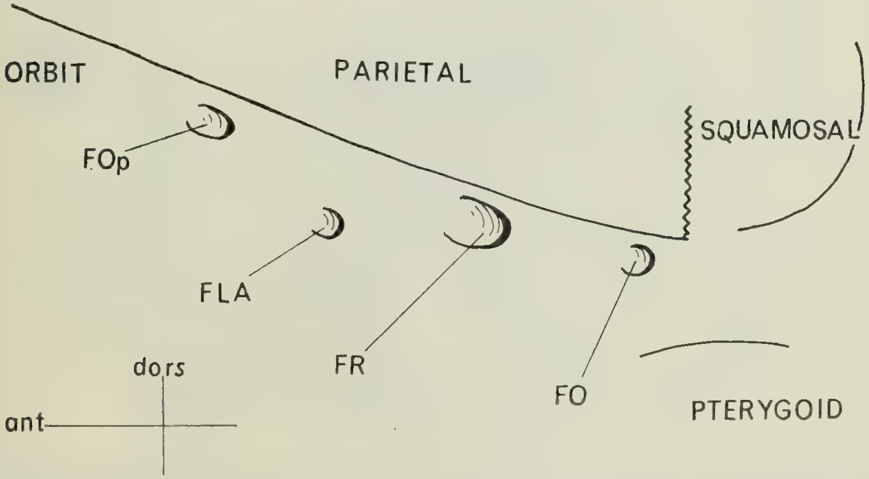


FIG. 6. *Megistotherium osteothlastes* gen. et sp. nov. Left sphenoid showing openings for cranial nerves. FLA = foramen lacerum anticus VI + V_1; FO = foramen ovale V_3; FOp = foramen opticum II; FR = foramen rotundum V_2.

paroccipital and postglenoid processes accommodated the external auditory meatus. The elongate glenoid carries the ramus of the squamosal far out laterally before it curves anteriorly to join the ramus of the jugal. The zygomatic arch is notable for being extremely wide and stoutly built, although the height of the bone dorso-ventrally is proportionately not as great as in for example *Patriofelis*.

Ear Region. The course of the external auditory meatus is horizontal along a passage between the postglenoid process and the paroccipital process. As in all creodonts, there is no tympanic bulla and no indication that one was ever present. A small triangular window around the sphenoid, exoccipital and squamosal reveals the petrosum. A small protuberance on the anterior face of the exoccipital may have

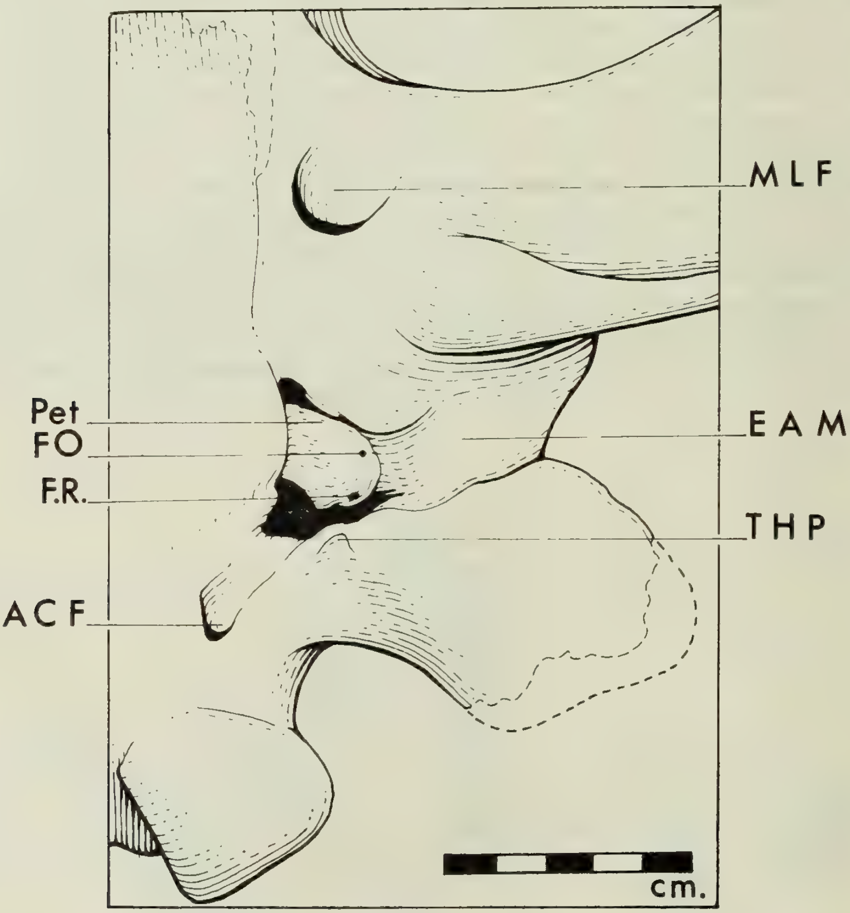


Fig. 7. *Megistotherium osteothlastes* gen. et sp. nov. Left ear region, ventral aspect. ACF = anterior condylar foramen; EAM = external auditory meatus; FO = fenestra ovale; FR = fenestra rotunde; MLF = medial lacerate foramen; Pet = petrosum; THP = tympanohyal process.

served for posterior attachment of a tympanic ring. The left petrosum is complete and the right broken to reveal the cochlea with probably three spiral turns. The identification of the openings is shown in Fig. 7.

Sinuses. Sinuses make up a large proportion of the skull volume, much more than in any other known carnivorous mammal. The brain is completely surrounded by sinuses, dorsally, laterally and ventrally. In specimen M 26515 the area of sinuses seen in transverse section immediately anterior to the sella turcica is 2·6 times greater than the area of the brain (16·25 cm^2 to 6·25 cm^2). In the domestic cat a section in the same area shows the brain to be five times greater than the sinuses. According to Paulli (1900) the extent of pneumaticity is dependent on skull size; large skulls have greater pneumaticity. The sinuses are extensive in bears, and in the giant panda *Ailuropoda* the sinuses make up a greater volume than the brain (Davis 1964). The differential in *Megistotherium* is even greater due partly to the large size of the fossil species and partly to the smaller creodont brain.

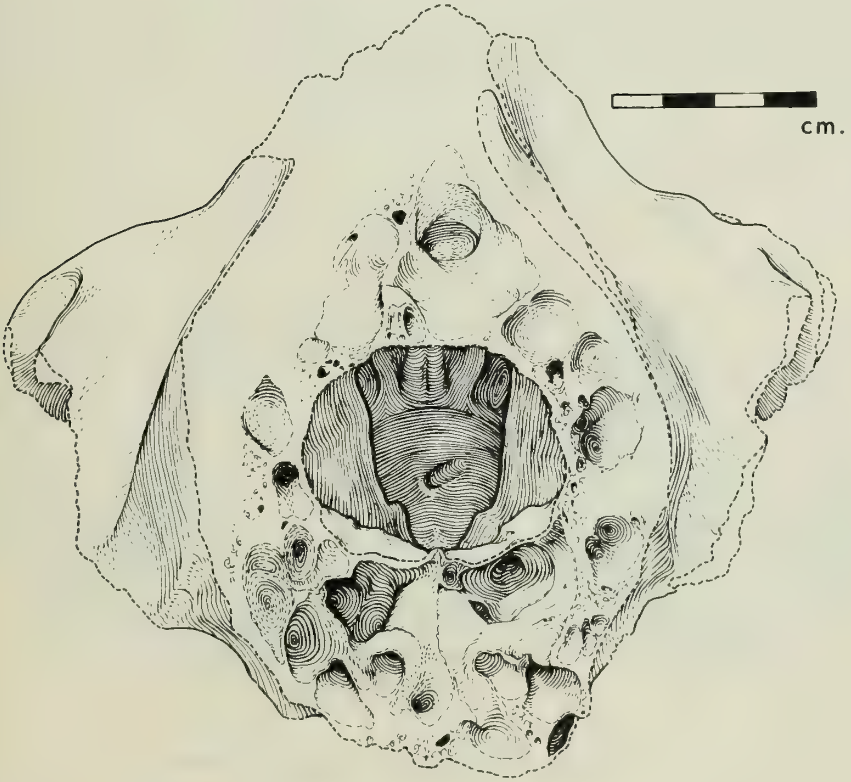


FIG. 8. *Megistotherium osteothlastes* gen. et sp. nov. Transverse section of cranium (M26515) showing sinuses; viewed from front.

Brain. The endocast taken from specimen M26515 shows that the brain was basically similar to that of *Hyaenodon* and *Pterodon,* though larger and rather more complex. The olfactory lobes and the anterior of the cerebrum are lacking and the volume of the remaining brain is around 280 cc; thus the total brain volume cannot have been less than 300 cc but may have been over 400 cc.

The cerebrum has a well developed series of sulci, four from the median line to the pyriform lobe. The sulci are traversed by a series of blood vessels which give the whole a chequerboard appearance. Unlike *Pterodon,* the pyriform lobe is well developed. The tentorium separating the cerebrum from the cerebellum is inclined to the brain axis at 50°; this steep angle allows for a larger cerebrum and it completely masks the mid brain and no trace of the quadrigeminae are visible, a feature which is markedly different from *Hyaenodon* and *Pterodon* in which the quadrigeminal tubercles are exposed. The cerebellum is large, occupying perhaps as much as 25% of the brain volume; it is clearly divided into vermis and two lateral lobes, and their surface is corrugated. On the ventral surface the beginnings of the olfactory tracts can be seen anterior to the optic chiasma. The hypophysis has no definable lateral extent and appears to merge with the optic tracts, between which can be seen the loop made by the oculomotor nerve. Lateral to this the trigeminal and facial nerves issue. There is no distinct pons varolii and in this region the medulla oblongata is obscured only by the passage of the pyramidal tracts.

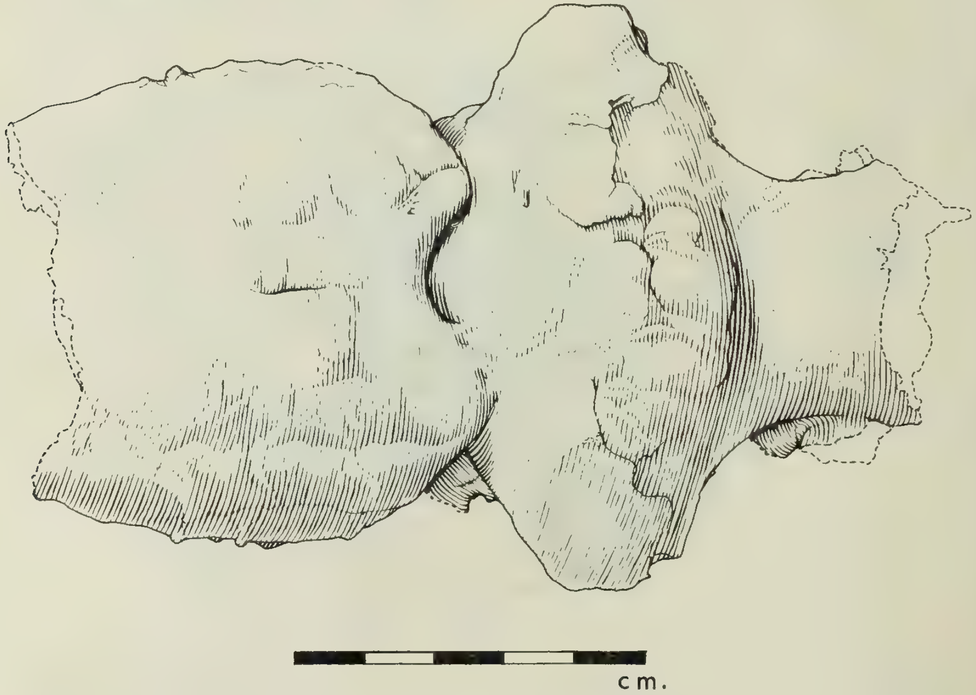


FIG. 9. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Dorsal aspect. From cranium (M26515), Gebel Zelten.

There are few accounts of creodont brains for comparison; the brain of *Megistotherium* retains a number of primitive characters, but displays in the cerebrum and cerebellum more complexity than is usual in creodonts.

Dentition. The dental formula for the upper dentition is 1 1 4 3. This differs from normal hyaenodonts only in the great reduction of the incisors to one. The teeth are poorly preserved but sufficient survives to establish most of the salient features.

The single incisor is very large and probably the third; it is absent on the right and only the root remains on the left side. The transverse section of the tooth just below the base of the crown is egg-shaped, the point directed anteriorly. The incisors are closely juxtaposed and stand proud, anterior to the canines.

The canine is missing on both right and left sides, but the alveolus betokens its enormous size, massive root and near circular transverse section.

The first premolar is missing on both sides; it was a small single rooted tooth placed behind and slightly medial to the canine. The rest of the cheek dentition, P^2 to M^3, lies on a straight line; this line if continued anteriorly would pass through the incisor tooth on the opposite side. The angle between the line of the right and left cheek dentition is 50°. Almost the whole of the second premolar is preserved on the left side; the root is doubled and the crown single cusped. The crown of P^2 is longer than broad, has a posterior keel, thick enamel. and the tip of the cusp is worn flat so that overall the tooth resembles P^2 or P^3 of *Crocuta*. Small diastemae separate P^2 anteriorly and posteriorly from P^1 and P^3. P^3–M^3 form a tight series without any gaps between the teeth. Of P^3 only the roots survive and the tooth is notable in possessing three roots, each of equal size; the internal root is opposite

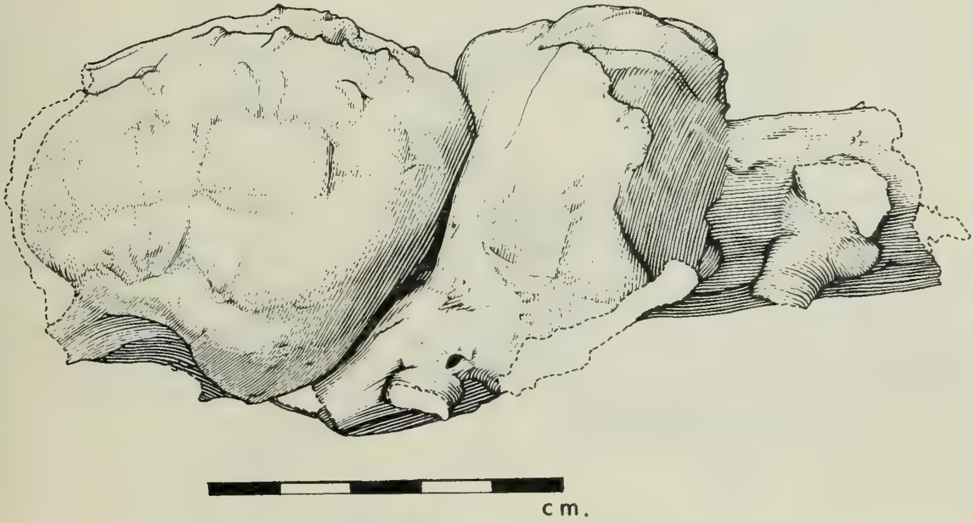


FIG. 10. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Lateral aspect. From cranium (M26515), Gebel Zelten.

the posteroexternal and not anteroexternal root, and the tooth length was apparently slightly greater than the width. From the three roots preserved on the left side P^4 appears to have been a larger version of P^3, although the transverse width across the root is greater than their length. On the right side the anterior root has been resorbed and the internal root is in process of being resorbed; this condition may relate to the bone pathology.

Only the roots of M^1 survive; the posterior root is the largest and the internal root is opposite the anteroexternal root. The slightly larger size of the internal root would suggest that the protocone was rather larger than the paracone. The second molar was the largest cheek tooth and is partially preserved on both sides; the tooth closely resembles in pattern the first (not second) molar of *Pterodon*. The paracone and metacone are connate but distinguishable and succeeded by a stout shearing metastyle; there is a small parastyle and well developed protocone; the tooth is considerably longer than broad. The third molar was a small two-rooted transverse tooth, again much as in *Pterodon*, although known only from root fragments.

Post-cranial Skeleton.

In the absence of associated remains, the attribution of post-cranial bones is rarely easy, often difficult and frequently impossible. The bones described below are for the most part indubitable creodont carnivore and their size distinguishes them from small species in the same beds.

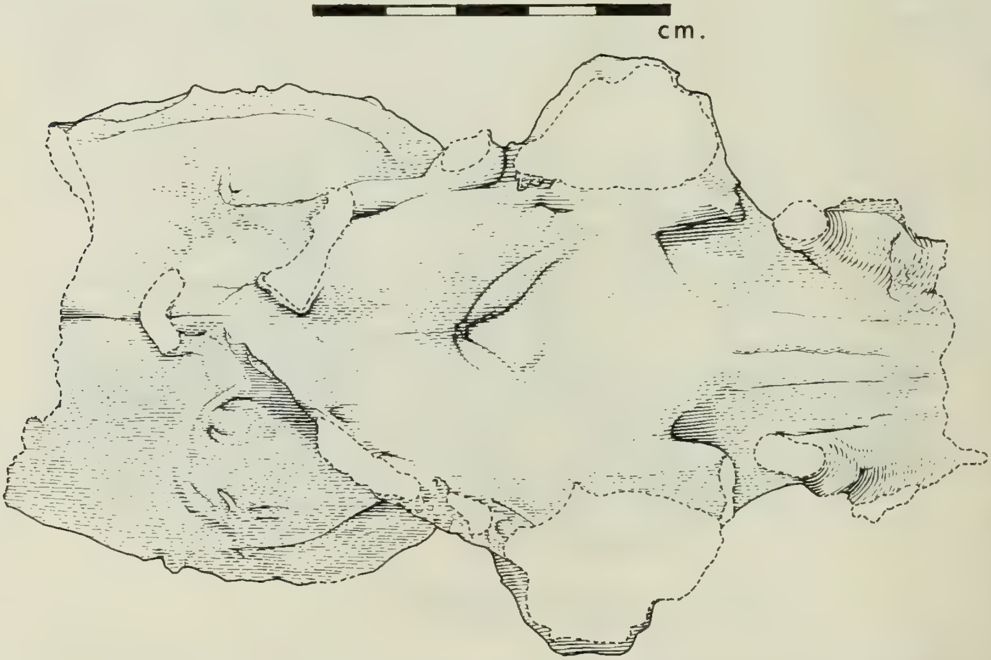


FIG. 11. *Megistotherium osteothlastes* gen. et sp. nov. Brain endocast. Ventral aspect. From cranium (M26515), Gebel Zelten.

Atlas. Specimen M21902 is the only indubitable vertebra of *Megistotherium*. It is essentially similar to that of *Hyaenodon* which differs but little from a canid atlas. The transverse process is greatly expanded in *Megistotherium*, which gives the bone a similarity to that of rhinoceros. The posterior margin of the process is greatly thickened to form a strong strut. On the ventral surface of the neural arch the longus colli tubercle is well developed while the dorsal surface of the arch is heavily scarred by the origin areas of the rectus capitis muscles. The cotyloid facets are deeply curved and firmly enclose the occipital condyles. The posterior axial facets are circular and flat (a distinguishing feature from rhinoceroses where the facets are ovoid and concave). The vertebral canal opens posteriorly close to the axial facet, and anteriorly has a large opening on the ventral surface of the wing. The oblique foramen is situated relatively close to the anterior margin of

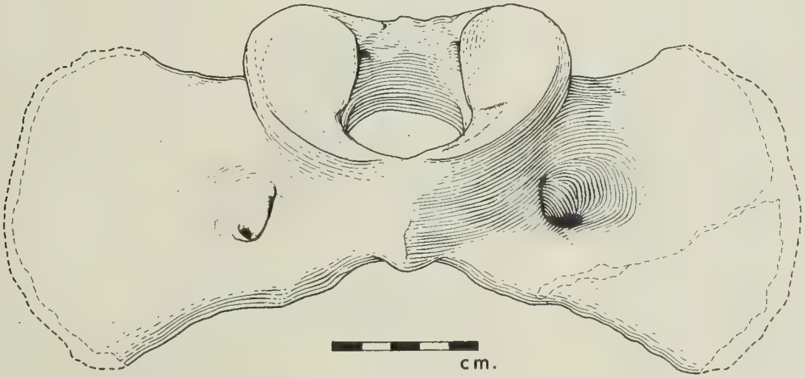


FIG. 12. *Megistotherium osteothlastes* gen. et sp. nov. Atlas. Dorsal aspect. (M21902), Gebel Zelten.

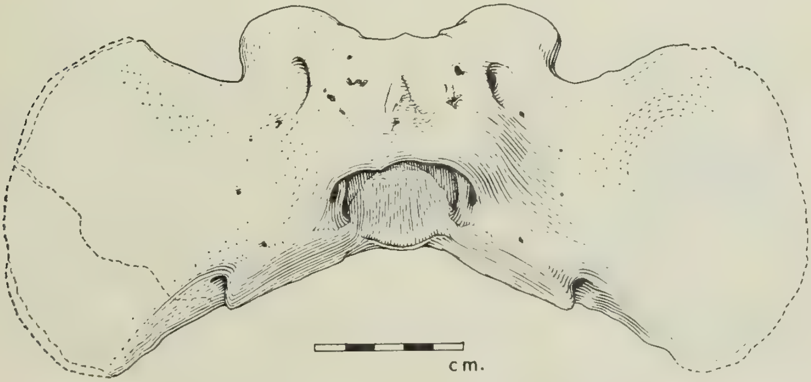


FIG. 13. *Megistotherium osteothlastes* gen. et sp. nov. Atlas. Ventral aspect. (M21902), Gebel Zelten.

the neural arch and a wide alar notch allows for the passage of the ventral root of the first spinal nerve. Within the neural arch can be seen the pit for the transverse ligament and an opening for a branch of the vertebral artery.

The wide alar processes and stout posterior border signal a heavy obliquus and longissimus musculature for lateral and upward head movements.

Humerus. The humerus is known only from two incomplete distal ends. The entepicondyle appears to have been larger than the ectepicondyle. The entepicondylar foramen is long and narrow; the olecranon fossa is deep and the trochlea spans about 270°.

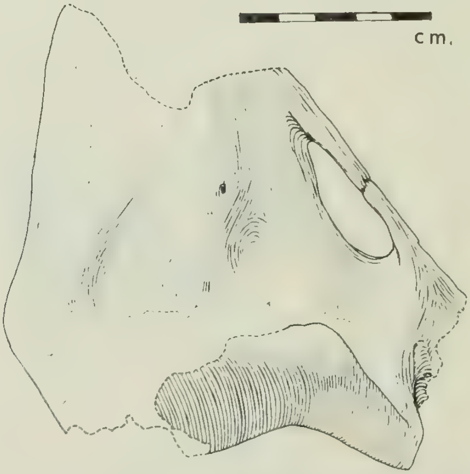


FIG. 14. *Megistotherium osteothlastes* gen. et sp. nov. Right humerus, distal end. Anterior aspect. (UB20576), Gebel Zelten.

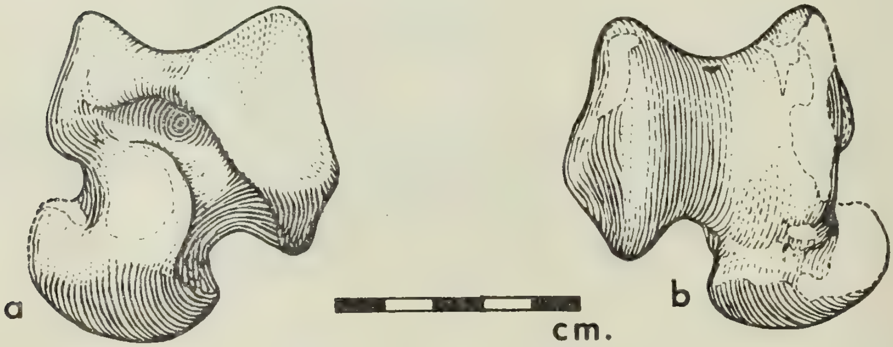
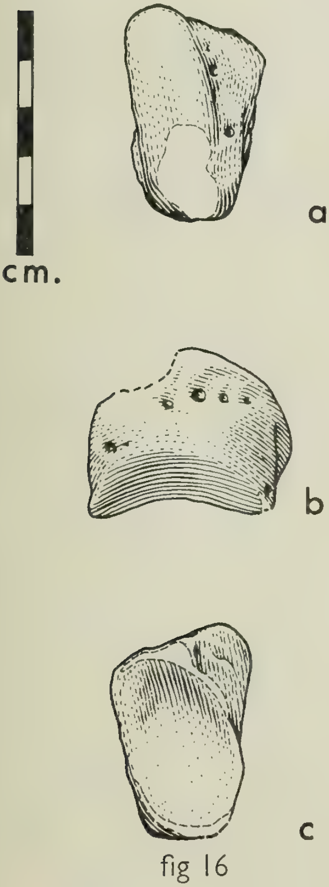


FIG. 15. *Megistotherium osteothlastes* gen. et sp. nov. Right astragalus. (UB20579), Gebel Zelten. (a) Distal aspect. (b) Proximal aspect.

Astragalus. The bone is typically creodont. The trochlea groove is asymetrical, the lateral border high and the fibular articulation facet prominent. The astragular foramen has a small opening on the trochlea surface, but a large distal opening between the calcar facets at the head of a deep groove for the interosseous ligament. The head, carried obliquely on a short neck, has a large convex navicular facet. Specimen UB20578 is a left magnum, and from its size probably referable to *Megistotherium.*

Metapodials. Four metapodials, two of them poorly preserved, are referable to *Megistotherium;* all are probably metatarsals and two are likely to be the third.



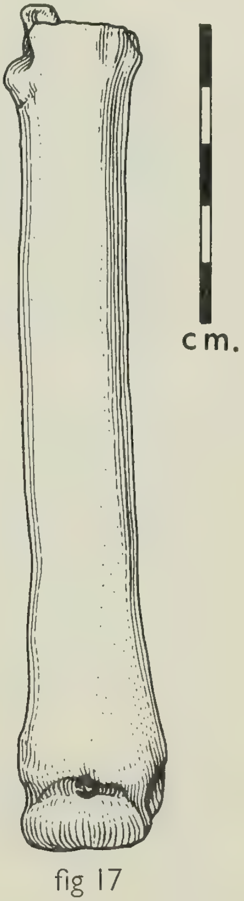


FIG. 16. *Megistotherium osteothlastes* gen. et sp. nov. Left magnum. (UB20578), Gebel Zelten. (a) Proximal aspect. (b) Lateral aspect. (c) Distal aspect.

FIG. 17. *Megistotherium osteothlastes* gen. et sp. nov. Metapodial. (UB20580), Anterior aspect.

TABLE I

Measurements.

Megistotherium osteothlastes gen. et sp. nov.

Type specimen M26173

Occlusal aspect	*cm*
Maximum transverse width across occipital condyles	9·3
,, ,, ,, ,, paroccipitals	ca 22·9
,, ,, ,, ,, zygoma	47·1
Maximum length, premaxilla—occipital condyles	66·4
Maximum width at level of M³	24·1
,, ,, ,, ,, ,, P²	8·5
,, ,, ,, ,, ,, C	15·1
,, ,, ,, ,, ,, I	5·9
Dorsal aspect	
Maximum width between external auditory meati	17·6
,, ,, ,, infraorbital foramina	11·1
Length of sagittal crest	ca 31·0
Lateral aspect	
Dorsoventral height of infraorbital foramen	3·0
,, ,, from palate at P¹ to nasal	12·1
Posterior aspect	
Height from roof of foramen magnum to sagittal crest	19·4
Dorsoventral height of foramen magnum	3·4
Transverse width of foramen magnum	4·1

Dentition		*cm* anteroposterior	transverse
Incisor	(alveolar)	3·2	2·0
Canine	(,,)	6·0	3·8
,,	depth of root 8·7		
P¹	(alveolar)	1·8	1·4
P²	(crown)	2·8	1·7
,,	crown height 1·6		
P³	(alveolar)	3·4	3·2
P⁴	(,,)	3·3	4·0
M¹	(,,)	4·1	3·4
M²	(crown)	4·6	3·9
M³	(alveolar)	1·3	3·0

Second Skull M26515–26518

Maximum transverse width across occipital condyles			9·1
Maximum width transverse across paroccipitals			20·0+
Dorsoventral height of foramen magnum			3·2
Transverse width of foramen magnum			3·5
Dentition		anteroposterior	transverse
Incisor		—	1·9
M²	(alveolar)	4·0	3·9
Post-cranial			
Atlas: maximum width across alar processes			26·5
Humerus: maximum distal width		est.	12·3
Astragalus: trochlea width			5·6
Magnum: long axis length			4·0
Metapodial UB20580 maximum length			14·0
,, ,, width distal condyle			2·3

III. DISCUSSION

Weight. The skull of *Megistotherium* directs comparison among living carnivores with hyaenas, bears and the larger cats; the fossil has no single analogy among the present day stock and hence an attempt to reconstruct the whole animal from so few postcranial remains would be futile. Estimates can however be made of weight. Jerison (1961) made a revised statement of Dubois's formula for the ratio of brain/body weight, incorporating in it a constant which varied through the Tertiary. Jerison expressed the formula as $E = kP^{2/3}$, where E is the brain weight, P the body weight and the value of k varies from 0·03 for Eocene to 0·12 for Recent. On the evidence of the endocranial cast it is known that the cranial capacity of *Megistotherium* cannot have been less than 300 cc. Substituting 300 g for E in the equation gives a body weight P of 1,000 Kg.

A second estimate is based on the use of the humerus. The distal width of the humerus in *Megistotherium* (12·3 cm) is equal to that in a large brown bear, though the largest bears have humeri in excess of this (12·6 cm recorded on a British Museum specimen). Individuals of *Ursus arctos* are known to reach 780 Kg; although it has not been possible to correlate directly individual weights and humeral widths; it seems reasonable to suggest that a bear with a humeral width of 12·3 cm could

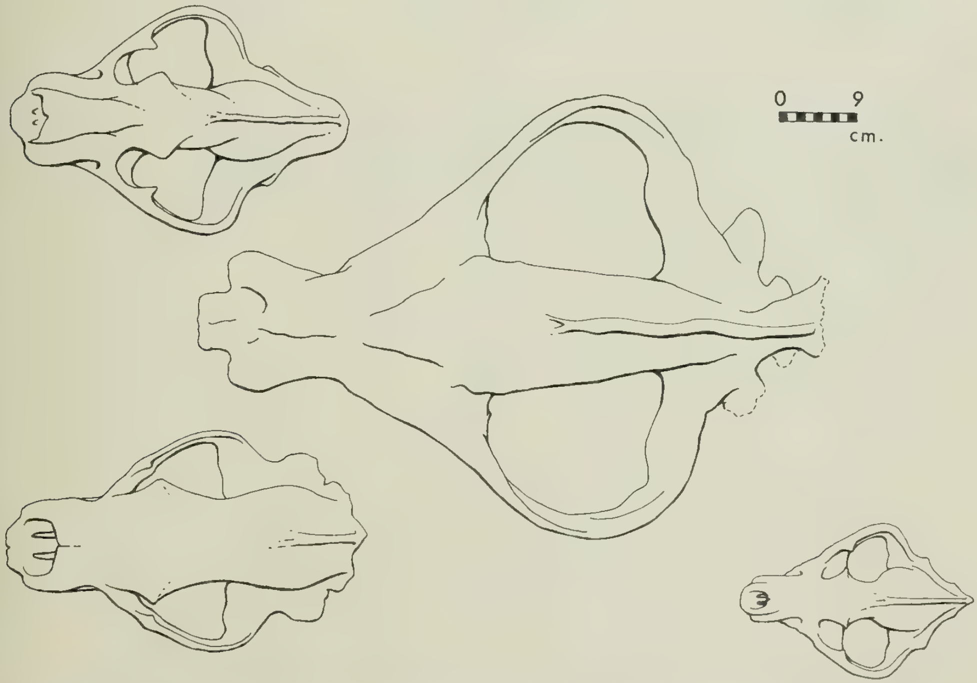


FIG. 18. *Megistotherium osteothlastes* gen. et sp. nov. Holotype skull compared with lion, bear and hyaena skulls.

weigh around 760 Kg; this estimate assumes body proportions not dissimilar to bear. It is unlikely that a carnivore as large as *Megistotherium* could gallop like lion or hyaena and the bear analogy seems reasonable.

The hyaenodonts have unusually large heads in proportion to their bodies; this would make the first estimate too high and the second too low. Taking this factor into account the most likely figure is around 880 Kg. for *Megistotherium.*

From the above estimates the brain/body weight ratio in *Megistotherium* is 1/3,000. Since body weights are highly variable in a species, the ratio is subject to considerable fluctuations. Few sources give the necessary data to measure this variation, but among them must be singled out the superb recent work of Brauer & Schober (1969). The pertinent examples are:—

Table II

Species	Body weight grams	Brain weight grams	Ratio	Source
Thalarctos maritimus	450,000	509	1 : 880	B & S 1969
Ursus arctos	200,000	296	1 : 675	,,
Panthera tigris	180,000	315	1 : 570	,,
,, *leo*	155,000	241	1 : 640	,,
,, ,,	119,500	291	1 : 545	Weber 1927
Crocuta crocuta	75,000	165	1 : 450	R.J.G.S.

The *Ursus* example was only half the weight of the *Thalarctos;* brown bears are known to exceed polar bears in weight and the heaviest polar bear is nearly double the example. The two examples of lion show a wide difference in ratio. The hyaena is based on a cranial capacity measurement of a large individual and a weight based on figures in Walker (1968). However even allowing for all these variables, the ratio in *Megistotherium* is lower by a factor of two or three.

Functional analysis of the jaw and dentition. The whole architecture of the skull of *Megistotherium* is moulded for maximum efficiency in feeding. The most striking feature is the enormous temporal musculature, witnessed by the very wide zygoma together with the high and long sagittal crest. The weight of each temporal muscle was probably around 10 Kg. The zygomatic arch while wide is not excessively heavy as in for example *Patriofelis* (see Denison 1938, fig. 19). This implies that the masseter was not developed to the same extent and the temporal was, as in most carnivores, the major muscle used in jaw closing. Turning now to the dentition let us examine how this musculature could have been used to best effect.

In *Megistotherium* M^3 is vestigial and M^{1+2} are carnassial. These latter teeth could be compared with the powerful and efficient carnassial P^4 in *Crocuta* and *Panthera.* Crusafont & Truyols (1956) have given a quantitative measure of the degree of carnassality in the different families of fissipeds. This measure is based on the angle formed on P^4 between protocone-metacone and paracone-metacone. The more carnivorous species have small protocones and longitudinal shears and hence low angles. In tiger the angle is 13°, in hyaena 15°. In the Oligocene hyaenodont *Hyaenodon mustelinus* the angle is also 15° on the carnassial. In both *Pterodon* and *Megistotherium* the angle rises to 35° indicating a considerable loss of shearing efficiency. Further the size of the carnassials in *Megistotherium* is proportionately small. None of this suggests that the temporal musculature was developed primarily to operate on the carnassial dentition.

Megistotherium has like *Crocuta* heavy blunt premolars. In *Crocuta* P^3 is used in bone crushing and can exert a pressure of 1 ton per cm^2; as the tooth crown has an area around 0·5 cm^2, this means an effective pressure of about half a ton, which is approximately 2·5 times greater than the pressure man can exert on his back molars. It is not possible to make a precise calculation for *Megistotherium*, but is likely that the P^{3+4} were not less efficient than in *Crocuta*.

The canine of *Megistotherium* is unfortunately missing, but the alveolus indicates that it was large, stout and ovoid. The canines from Kenya are exactly the shape and size one would expect for *Megistotherium*. The efficiency of the canine is dependent on its size and proximity to the fulcrum (glenoid). Hence the facial shortening in hyaena and giant panda improve considerably the efficiency of the canine. (See Table III.) A remarkable feature of *Megistotherium* is the long face; even with this apparent disadvantage, the ratio of canine area to canine-glenoid length is greater than in any living fissiped. This suggests that the canine is the most important factor in food capture.

Smith & Savage (1959) gave an equation for the mechanical efficiency of musculature, $T = P \times \frac{a}{l}$ where T is the force exerted, P is the pull or tension in the muscle, and $\frac{a}{l}$ corresponds to the mechanical advantage of a lever, i.e. the ratio of the distance of the applied force from the fulcrum to the distance of the load from the fulcrum (see Fig. 19). In this case a is the moment arm of the temporal muscle, l the distance from the glenoid to the canine, and for P we can take the area of the temporal

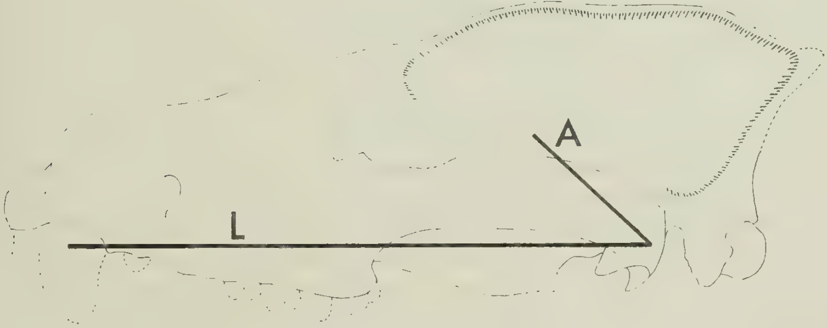


FIG. 19. Mechanics of the skull of *Megistotherium*. gen. nov. A = moment arm of the temporal muscle; L = distance from glenoid to canine.

muscle enclosed by the zygomatic arch. In Table III the last column gives the results of the substitution. It will be seen how very much more powerful is the canine of *Megistotherium* than that of any other species; five times greater than bear or tiger, and ten times greater than hyaena. However when a similar calculation is done for *Crocuta* on the P^3 it is seen to be much more powerful than the canine, and similarly when the P^4 in tiger is measured.

Finally there is the question why did *Megistotherium* maintain such a long jaw when it could have achieved similar power with much less effort had the jaw been shortened. Two arguments are possible; it is a genetical trait of the Hyaenodontidae to have long faces while their close relatives the Oxyaenidae had short faces. Secondly can be considered the likely prey; the large ungulates in the fauna are anthracotheres, pigs, rhinoceroses, mastodonts and deinotheres. The remains of proboscideans are much more abundant than any of the other taxa (see Savage 1968). *Mastodon angustidens* and *Prodeinotherium hobleyi* were about the size of living elephants, and also present was a smaller and much rarer species *Mastodon pygmaeus*. Without a skeleton it is impossible to determine how *Megistatherium* would have brought down its prey; it is likely to have had a good sense of smell and so long as it could move quicker than its prey no great turn of speed would be necessary. The wide and stout exoccipital processes and the large alar wings on the atlas point to the massive development of lateral musculature for turning the head sideways—or for resisting a struggling prey. In lion and tiger the mandible has a gape of around 50°, measuring the angle between the upper and lower dentitions Although the mandible of *Megistotherium* is unknown and assuming no exceptional specialisations, it is reasonable to except the gape to be similar. A gape of 50° in *Megistotherium* would give a clearance of 40 cm at the alveolar margin of the canines, or a clearance of 30 cm between the tips of the canines. Living elephants have a leg diameter of around 30 cm. Had *Megistotherium* a shorter jaw it would have been unable to bite into a proboscidean limb.

The incisors remain to be considered. Only one pair is present in the premaxilla, and these are large; if the Bugti specimen is correctly assigned, then the mandible possessed two functional pairs and possibly a vestigial third. Comparison is closest with *Sarkastodon*, the Mongolian oxyaenid second only to *Megistotherium* in size, (omitting *Andrewsarchus*, the mesonychid which was non-carnivorous and now classified among the condylarths). *Sarkastodon* was short jawed, had efficient shearing teeth and the incisor formula was $\frac{2}{1}$; in the premaxilla I^2 was vestigial and a large I^3 the only functional incisor. As in *Megistotherium* there is a diastema between the canine and incisor to allow for the accommodation of the lower canine. Denison (1938) in his excellent review of the group concluded the reduction of the lower incisors in *Sarkastodon* pointed to diminution of function; this may be true if the lower incisor was as small as indicated in his reconstruction, but can hardly apply to the upper. If *Megistotherium* used its canine as suggested above, then small incisors would be in danger of being broken by struggling prey or by occluding accidentally on bone. Reduction in number and increase in size is the best defence against this and also supplements the canine.

TABLE III

		Canine area (C) cm^2	$\frac{10 \times C}{l}$	Carnassial angle	$\frac{a}{l}$	P cm^2	$P \times \frac{a}{l}$
Ailuropoda		2·2	1·16		0·43	40	17·2
Thalarctos		6·1	2·65		0·28	58	16·2
Ursus		5·7	2·45		0·37	65	24·1
Megistotherium		22·8	4·47	35°	0·35	314	109·9
Hyaenodon mustelinus		0·45	0·41	15°	0·24	8·7	2·1
Crocuta	C	2·2	1·33	15°	0·36	28·3	10·2
	P^3				0·52		14·7
Panthera tigris	C	5·5	2·68	13°	0·34	59	20·1
	P^4				0·54		31·9
Panthera leo		5·3	2·65		0·37	61	22·6

IV. OTHER MATERIAL REFERABLE TO AND COMPARABLE WITH *MEGISTOTHERIUM*

Specimens which could be referred to the genus *Megistotherium* or the closely allied genus *Hyainailouros* are known from Africa, Asia and Europe.

Considering first the African specimens, material from Egypt and Kenya will be discussed. Fourtau (1920) described from Moghara, Egypt an upper third premolar which he named *Hyaena* sp. indet. (loc. cit. pp 91–92; fig. 62). Von Koenigswald (1947) re-examined the tooth and concluded it was an upper third premolar which he assigned to the genus *Hyaenaelurus* and gave a new specific name, *H. fourtaui*. The tooth has parameters which are very close to those of *Hyainailouros sulzeri* (see Table IV). In *Megistotherium*, only P^3 and P^4 are three-rooted, and both teeth are much larger than the Moghara specimen. Further, *Megistotherium* is clearly distinguished from *Hyainailouros* in having a P^4 whose width much exceeds the length. The author concurs with Von Koenigswald in placing the Moghara tooth in the genus *Hyainailouros*. While the Moghara fauna is apparently of similar age to that of Gebel Zelten (Savage & Hamilton 1972), with several species in common, the Moghara carnivore is unknown in the larger Gebel Zelten fauna.

Three very large canines are known from Kenya (Fig. 20a, b & c). It is not clear whether they are uppers or lowers and they are considered Hyaenodontidae indet. The specimen from Rusinga (R2–4, 232'49) comes from strata which yield a fauna which can be correlated with that of Gebel Zelten (Savage & Hamilton 1972). The other two teeth however come from Fort Ternan whose fauna is much younger and placed by Bishop et al. (1969) in the late Miocene, with radiometric age of around 14–15 million years. If correctly assigned, then these teeth represent another example of a late survival of hyaenodonts in Africa; this would not be unexpected as from Kenya and Pakistan we know of the survival of hyaenodontids in the Pontian (Savage 1965).

Andrews (1914) described and illustrated (loc. cit. p. 179, Plate II fig. 2) a left astragalus from Kachuku, Karungu, Lake Victoria. The specimen (M10635) is about the size of a lion astragalus and has an astragalar foramen. Andrews thought it might be creodont and compared it to *Apterodon.* The astragalus is very different in size and proportions from that of *Megistotherium,* and I would agree with him that it could belong to a creodont of about the size of *Apterodon.*

Savage (1965) described some material of *Pterodon africanus* from Kenya, and he referred three additional teeth to a new species, *P. nyanzae.* The teeth are very similar to those of *Hyainailourus sulzeri,* but slightly smaller and comparable with what would be expected of *H. fourtaui.* My present view is that they should be transferred to the genus *Hyainailourus* and the specific name retained until further evidence is available.

Five specimens from the Bugti Beds of Pakistan arrest our attention. Forster Cooper (1924) described and figured a mandible (M12049) as *Anthracotherium ingens.* The specimen is patently not an anthracothere but could belong to *Megistotherium,* of a species rather larger than *M. osteothlastes.* The specimen has a large canine which recalls the Rusinga specimen mentioned above. The evidence of the alveoli suggests three incisors were present. The I_1 alveolus is preserved on both sides and that of $I_{2\&3}$ on the left side only. The alveoli decrease in size toward the canine, and the third incisor has a small alveolus almost tucked under the canine. Immediately behind the canine is a deep alveolus suggesting the presence of a single

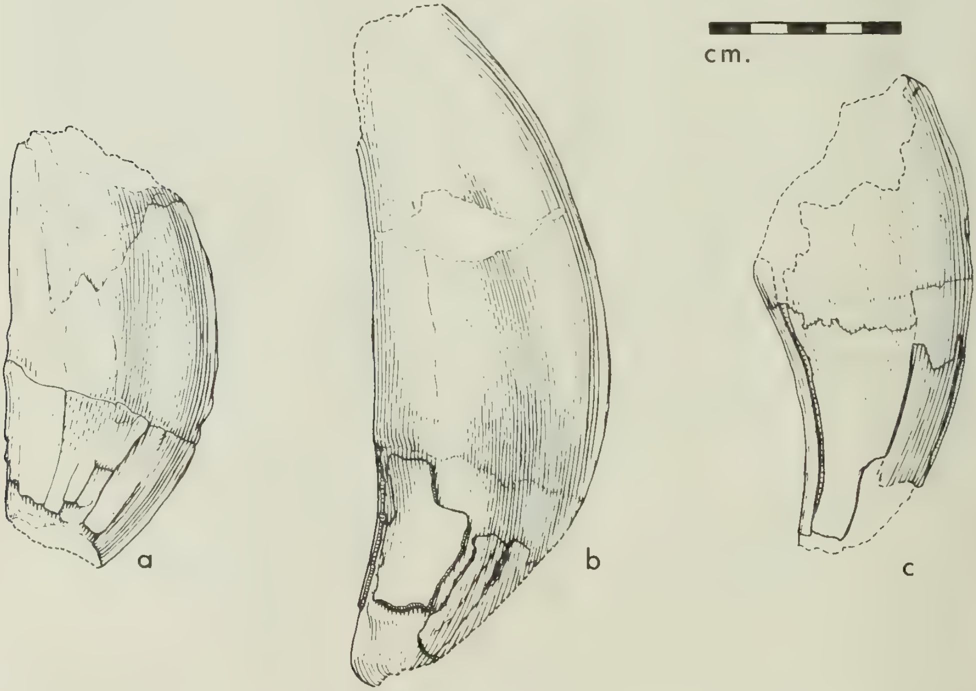


FIG. 20. Hyaenodontid canines. (a) R 2–4, 232 '49. (b) FT 2 '59. (c) FT 11 '59.

rooted P_1. $P_{2\&3}$ are well preserved double rooted teeth with well developed cingula anteriorly and posteriorly, the third premolar being a larger version of P_2. Without further evidence the author would hesitate to give a specific determination, and will assign it to *Megistotherium* sp. indet.

Pilgrim (1912 and 1932) described four creodont specimens from the Bugti Beds. In his 1912 paper all were assigned to *Pterodon*, but in 1932 he re-allocated two specimens to the genus *Hyainailouros*, a third *Amphicyon* and the fourth he regarded as indeterminate. Specimen D 107, is the type of *Hyainailouros bugtiensis* and I regard the two teeth in the mandibular fragment as $M_{2\&3}$; the species has a resemblance to the European *H. sulzeri*, but I would accept Pilgrim's opinion that it be retained as a separate species. I would also assign to *H. bugtiensis* specimen D 109 which I regard as a P_4 and which Pilgrim (1932) left as indeterminate. Specimen D112 is a toothless mandibular symphysis and I concur with Pilgrim in assigning it to *H. bugtiensis*. Specimen D108 was named by Pilgrim in 1912 as *Pterodon* sp., but in 1932 he assigned it to *Amphicyon shabazi* and with this transfer to the fissipeds I also concur. Pilgrim (1932) described a new species of *Hyainailouros* from the Kamlial Stage of the Attock District, Salt Range: *H. lahiri* comprises a mandibular ramus with the last two teeth preserved. Pilgrim regarded these as P_4 and M_1 and hence concluded it was a very large species. If however the teeth are interpreted as M_2 and M_3, which seems more plausible, then the specimen conforms closely to the type of *H. bugtiensis* and I see no reason why it should not be synonymised with the Bugti species.

In summing up, we can now point to the radiation of three genera of large mid Tertiary hyaenodonts. *Pterodon* is the smallest of the three and its species and their distribution were recorded by Savage (1965). The genus occurs in North America, Eurasia and Africa and ranges in time from Mid Eocene to Early Miocene; species are all strikingly similar and vary mainly in size. *P. grandis* from the Oligocene White River Beds of Saskatchewan is the largest and may be more correctly placed in the genus *Hyainailouros*. *Hyainailouros* has until the present been regarded as the largest form; the genus is not well known and until Van Valen (1966) reclassified the Hyaenodontidae it was usually considered as an appendix to the Felidae. The type species is *H. sulzeri* Biedermann from the Vindobonian of Veltheim in Switzerland; specimens are known from Burdigalian, Vindobonian and even Pontian deposits in France, Germany and Switzerland. Although all may not with certainty be assigned to the type species, no other good species have been established. Beaumont (1970) has reviewed the type material of *Hyainailouros sulzeri* from Switzerland, and given a reinterpretation of the work of Helbing (1925) on the species. From the early Miocene of Egypt comes *H. fourtaui* and from a similar level in Kenya comes *H. nyanzae;* these species are of doubtful validity. All the Asiatic specimens can be referred to *H. bugtiensis*, probably a distinct species from *H. sulzeri* and more primitive than its European counterpart.

The new genus *Megistotherium* is a gigantic form with distinctive dental differences from *Hyainailouros*. Apart from the type area in Libya, a mandible from Pakistan is confidently assigned to the genus, but not determined specifically. *Megistotherium* is thus limited as far as is known to the Early Miocene of Africa and Asia.

Table IV

Upper Dentitions (*mm*)

		C	P^1	P^2	P^3	P^4	M^1	M^2	M^3
Megistotherium osteothlastes									
HOLOTYPE Libya	a.p.	60	18	28	34	33	41	46	13
	trs.	38	14	17	32	40	34	39	30
Hyainailouros fourtaui									
HOLOTYPE Egypt	a.p.				26				
	trs.				20				
Hyainailouros nyanzae									
M19091 HOLOTYPE Kenya	a.p.					30			
	trs.					24			
M19092 „	a.p.					29			
	trs.					24			
M19093 „	a.p.						—		
	trs.						28		
Hyainailouros sulzeri									
HOLOTYPE Veltheim	a.p.			27		34	38		
	trs.			23		26	29		
Hyaenodont indet									
R 2–4 232'49 Kenya	a.p.	51							
	trs.	32							
F.T. 2 „	a.p.	51							
	trs.	37							
F.T. 11 „	a.p.	51							
	trs.	37							

Lower Dentitions (*mm*)

		C	P^1	P^2	P^3	P^4	M^1	M^2	M^3
Megistotherium sp.									
M12049 Bugti	a.p.	7·0		36	38				
	trs.	4·9		21	23				
Hyainailouros bugtiensis									
HOLOTYPE D 107 Bugti	a.p.							42	55
	trs.							23	28
H. bugtiensis D109 Bugti	a.p.					27			
	trs.					15			
H. bugtiensis D236 Attock	a.p.							36	50
	trs.							25	32
H. sulzeri HOLOTYPE Veltheim	a.p.					24		41	51
	trs.					21		22	28

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PLATE 1

Megistotherium osteothlastes gen. et sp. nov.
Holotype (M26173), Gebel Zelten.
Dorsal aspect ×$\frac{1}{4}$ approx.

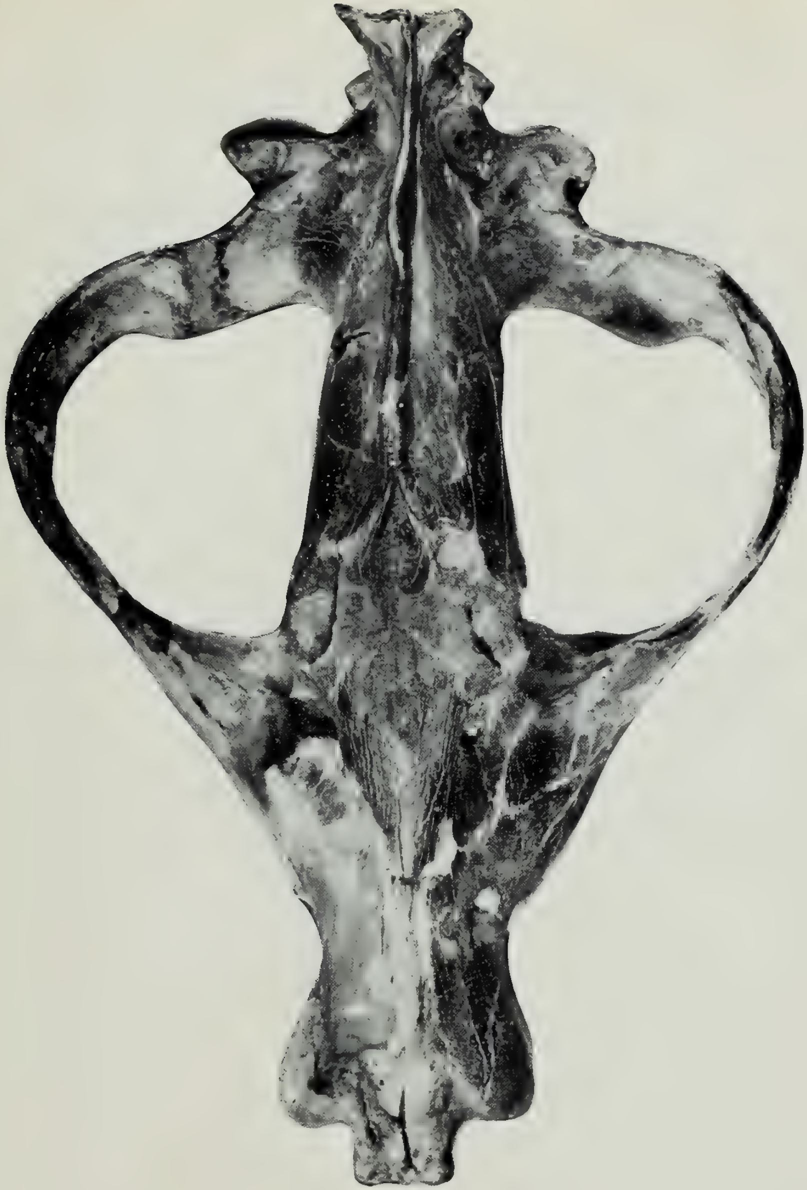


PLATE 2

Megistotherium osteothlastes gen. et sp. nov.
Holotype (M26173), Gebel Zelten.
Ventral aspect ×¼ approx.

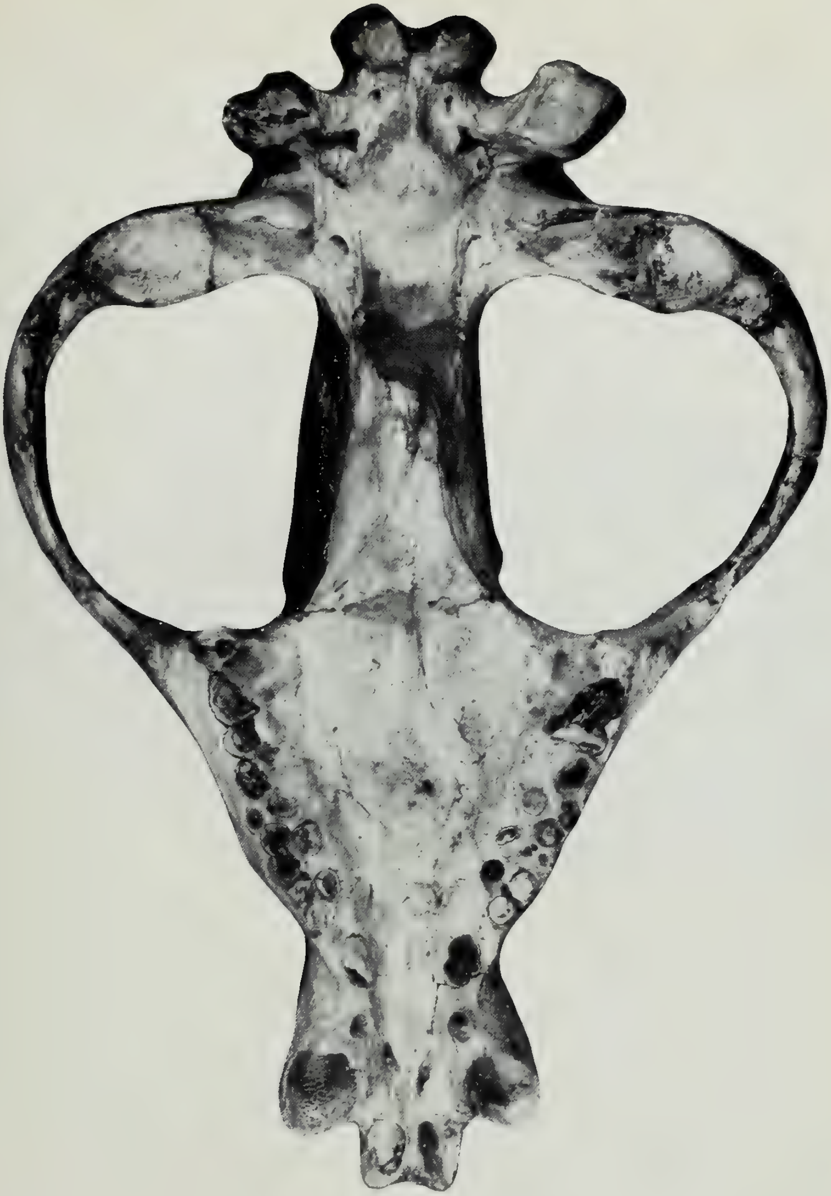


PLATE 3

Megistotherium osteothlastes gen. st sp. nov.
Holotype (M26173), Gebel Zelten.
Lateral aspect ×$\frac{1}{4}$ approx.

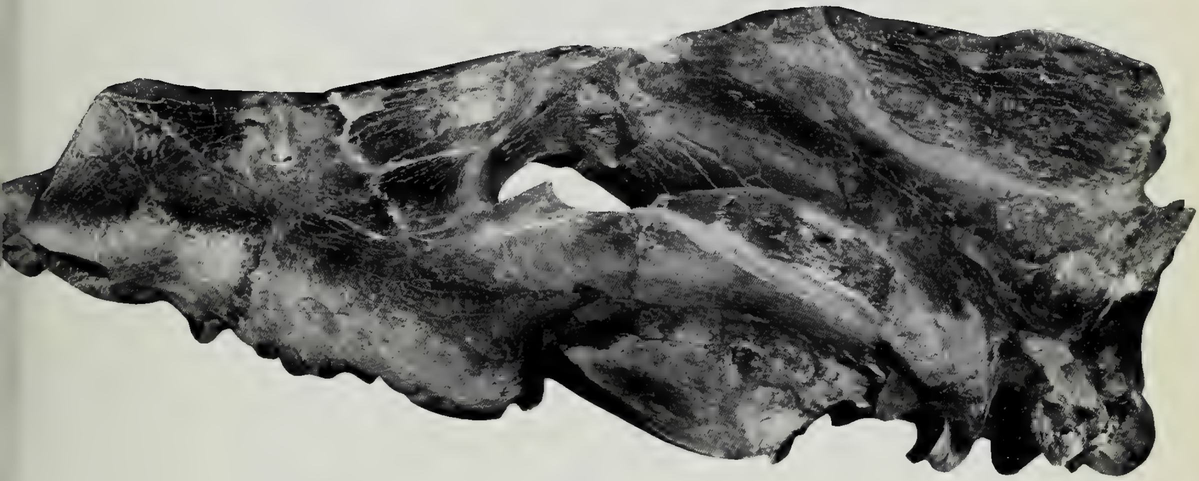
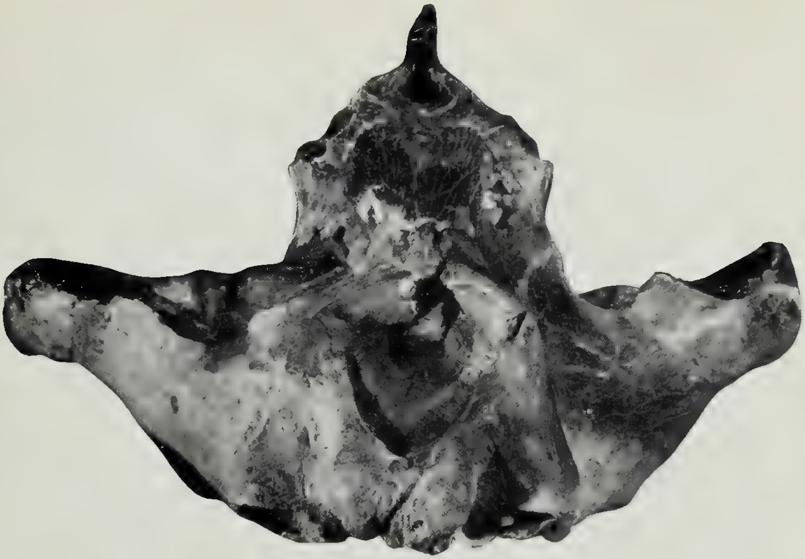
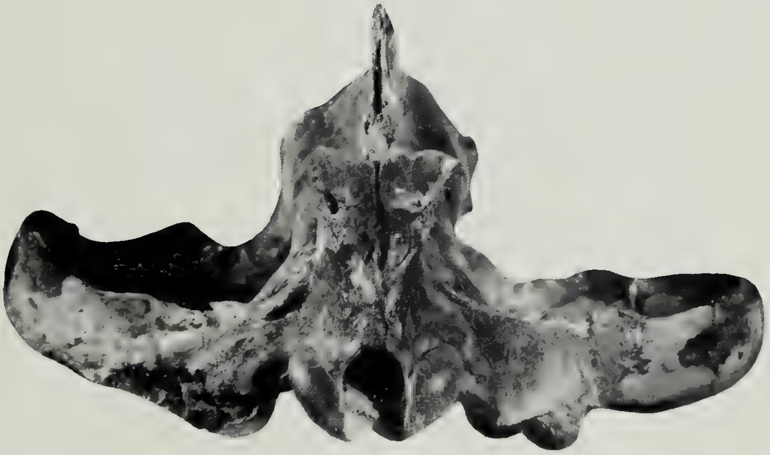


PLATE 4

Megistotherium osteothlastes gen. et sp. nov.
Holotype (M26173), Gebel Zelten.
(a) Anterior aspect; (b) Posterior aspect × ¼ approx.





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INTRODUCTION TO THE MIOCENE MAMMAL FAUNAS OF GEBEL ZELTEN, LIBYA

BY
R. J. G. SAVAGE
Department of Geology, University of Bristol
AND
W. R. HAMILTON

Pp 513–527; 3 *Text-figures*

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INTRODUCTION TO THE MIOCENE MAMMAL FAUNAS OF GEBEL ZELTEN, LIBYA

By R. J. G. SAVAGE & W. R. HAMILTON

ABSTRACT

An account is given of the occurrence of Miocene mammals at Gebel Zelten, central Libya. The geographical and geological settings are summarized, the history of the exploratory work reviewed, the composition of the fauna and flora is discussed, and the probable environment and age of the succession are assessed.

GEOGRAPHY

Gebel Zelten lies about 200 km south of the Gulf of Sirte (Fig. 1.). It consists of an elongate mesa which runs northwest—southeast, for about 140 km at 19° 30′–20° 30′ E., 28°–29′ N. The Esso Petroleum Zelten camp lies to the north of the gebel and the Oasis Waha camp lies to the south, the road joining these camps crosses the gebel at its narrowest point where it is only 8 km wide. In the west the gebel rises 40–60 m above the Zelten Rambla (sand sea); it dips gently to the east and blends with the Calenscio Serir (gravel plain) at its eastern end. The plateau is capped by a marine sandstone which is early Miocene in age and the edges are dissected by steep-walled wadis up to 3 km in length. It is in these wadis that many of the vertebrate remains are found, though some of the sites are on washout areas from the wadis.

HISTORY OF DISCOVERY

The first geological party to see the area was the Italian Scientific mission to Kufra in 1931, under the leadership of Professor Ardito Desio. Desio (1935) gave the name Marada Series to the succession of the Dor el Marada, 50 km northwest of Gebel Zelten. Desio's type section at Garet el Mazzala is about 80 metres thick and comprises mainly shales with interbedded sands and limestones; he recorded gypsum layers and a fauna of marine invertebrates and fish. The Italian route to Kufra, (still marked by fusti posts), lay along the western borders of the Gebel Zelten. On the basis of the shelly fauna Desio considered the Marada Series to be Langhanian (= Burdigalian) and Helvetian. Desio was probably only able to spend a very short time at Gebel Zelten and was unfortunate not to find any higher vertebrates. The two places where the fusti posts come closest to the

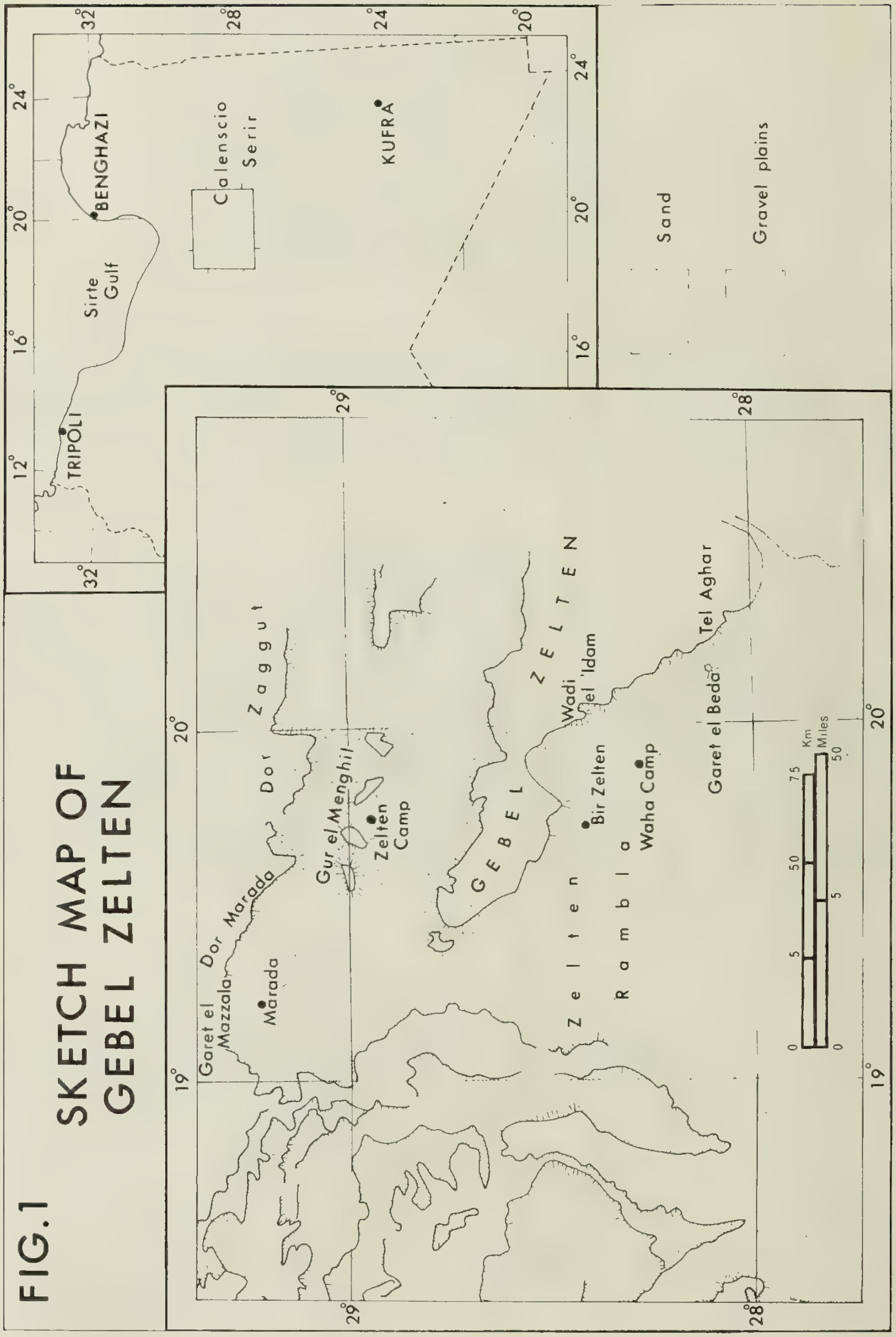

FIG.1 SKETCH MAP OF GEBEL ZELTEN

32°
28°
24°
20°
24°
20°
16°
12°
32°
24°
20°
16°
TRIPOLI
Sirte Gulf
BENGHAZI
Calenscio Serir
KUFRA
Sand
Gravel plains
19°
20°
29°
28°
Garet el Mazzala
Marada
Dor Marada
Dor Zaggut
Gur el Menghil
Zelten Camp
GEBEL ZELTEN
Zelten Ramla
Bir Zelten
Waha Camp
Wadi el 'Idam
Tel Aghar
Garet el Beda
Km
Miles
0
5
50
75
0
5
50

escarpment, (at Bir Zelten and Tel Aghar), are barren of fossils, not being near any of the river channels. Desio did however suggest the Zelten sandstone succession was in part contemporary with the Marada succession and equivalent to Aquitanian-Langhanian transition.

In 1957 Savage, as a member of the British Ennedi Expedition, passed east of Gebel Zelten across the Calenscio Serir en route to Kufra, but no outcrops were seen. With the exploration for petroleum in the late 1950's, prospecting gradually moved south from the coastal belt. In 1960 M. Magnier, of the Compagnie des Petroles Total Libye, explored the Gebel Zelten and found the first mammalian fossils. In December 1960 Professor C. Arambourg visited the north side of Gebel Zelten with M. Magnier and spent 10 days collecting surface finds (Arambourg & Magnier 1961, Magnier 1962, 1967). Arambourg (1961a & b, 1963) later described some of the species recovered and now housed in the Museum d'Histoire Naturelle, Paris. During the following three years prospecting intensified, concessions were allocated and oil production commenced. Gebel Zelten falls into two concessions divided along the parallel 28° 30′ into a northern part in the Esso concession 6, and a southern part in Oasis concession 59. Colley (1964) summarized the regional setting of the geology.

In 1963 Dr R. C. Selley of Imperial College, University of London, commenced a series of visits to the Marada and Zelten regions to study the stratigraphical succession and the sedimentary history (Selley 1966, 1967 and 1969). In 1965 Dr H. Doust also of Imperial College commenced a study of the palaeoenvironment using especially invertebrate and trace fossils (Doust 1968).

The finding of bones by oil prospecting geologists aroused interest and invited detailed exploration. Three expeditions under the leadership of Dr R. J. G. Savage from the University of Bristol have concentrated on the vertebrate faunas of the Gebel Zelten area. In 1964 Savage accompanied by Mr M. E. White spent two months at Oasis Waha camp exploring the southern half of the Gebel Zelten. In 1966 Savage accompanied by Dr S. W. Taylor spent a month at the Esso Zelten camp exploring the northern half of the Gebel. In 1967 Savage accompanied by Dr J. M. Harris visited the northern and southern sides of the gebel and made further collections. In 1968 Savage accompanied by Dr. W. R. Hamilton briefly visited the area on their way south and made some additions to the collections. Preliminary reports are to be found in Savage & White (1965), Savage in Selley (1969) and Savage (1971), and the first monograph on ruminants is by Hamilton (1972).

GEOLOGY

The following account of the geology is taken largely from Selley (1966, 1969). In view of the detailed work of Selley no stratigraphic work was undertaken by the Bristol parties. The vertebrate collecting is regarded as complementary to the work of Selley on the sediments and of Doust on the invertebrate fauna.

During the late Mesozoic and Tertiary a series of shelves and basins developed on the northern edge of the Saharan shield in the Tethyan foredeep. The Sirte Basin was one of these basins which gradually became infilled as subsidence waned and the sea retreated northward during the Tertiary. The centre was infilled with shales while around the rim carbonate sediments were deposited. The marginal limestones are mainly of detrital organic origin and often dolomitized; fossils abound, especially oysters, corals, bryozoans, echinoids and foraminifera. Interbedded with the limestones are unfossiliferous shales, often gypsiferous. The limestones and shales are locally replaced shoreward by sandstones as in the region of Gebel Zelten. The majority of the oil and gas reserves are found in the marginal facies of the basin.

Selley has substituted the term Marada Formation for Desio's Marada Series and has included the Zelten succession in the formation. Selley (1966) recognised five major facies each with characteristic lithology, environment and fauna (Table I). Selley envisaged a series of offshore bars with lagoons behind, into which issued rivers depositing fluviatile sediments (Fig. 2). The reconstruction shows a major river flowing north through the Gebel Zelten area with distributaries on the north side of the escarpment. Selley produced a wealth of detailed quantitative analyses to support his interpretations, and compared the regime to that of the present day coast of Texas and the Trucial coast.

Doust (in Selley 1969) has cast doubt on the nature of the limestone reefs, suggesting the limestones formed as submarine banks, thus leaving the sea to invade the 'lagoons' with restricted circulation on intertidal flats. The nature of the fluviatile and estuarine environments is unquestioned.

Palaeontology

Doust (1968) has described the marine faunas in detail. Ichnofossils abound and the limestones are particularly rich in shelly faunas. In the broken ground of Gur el Menghil, between Dor Zaggut and Gebel Zelten, Doust was able to correlate beds on the occurrence of two marker bands, both close together near the middle of the section. The lower band contains abundant remains of the bryozoan *Idmonea fenestrata* Busk and two metres above is a band rich in the echinoid *Echinolampas*. These bands can be traced south into Gebel Zelten, where on average the invertebrate fossils are less abundant and the only common and widespread fossil is the oyster *Crassostrea gryphoides* (Schlotheim).

Apart from calcareous algae, plant fossils are very rare. Samples of matrix and coprolites were examined by Dr K. C. Allen of Bristol and Dr. D. K. Ferguson of Utrecht but no undoubted pollen was found. A few leaf fragments have been found, some of which are probably bog-myrtle (*Myrica integerrima*). The only fruit found were ground cucumbers (*Cucumeria*).

Silicified wood is virtually ubiquitous, not only in the Gebel Zelten, but throughout the Sahara, more or less regardless of the stratigraphic age of the beds where it is found, be they Mesozoic or Tertiary, marine or non-marine. The wood tends to be commonly in association with arenaceous facies. In a few sites wood was found to have borings; the holes are around half a centimetre in diameter. They could have been made by the marine worm *Teredo*, or alternatively they could be due to a tropical insect. In fifteen years of desert travel, Savage has rarely seen wood which is indubitably and stratigraphically *in situ*. In the instances where wood has

TABLE I

Summary of facies parameters (after Selley 1969)

Facies	Lithology	Distribution	Sedimentary structures	Fauna	Palaeocurrents	Supposed environment
1. Detrital limestones	Bioclastic calcarenites, rare calcirudites and calcilutites	Predominate in north	Massive, flat-bedded or cross-bedded, often bioturbated	Mainly marine	Bi-modal, major mode directed southwards (on-shore)	Off-shore bars and barrier beaches
2. Laminated shales	Calcareous shales and calcilutites	↑	Laminated or massive	Local oyster reefs	None	Lagoonal
3. Interlaminated shales and sandstone	Shales & silts; rare fine sands	↓	Interlamination, small-scale cross-stratification and bioturbation. Channelling. Lignites.	Mixed marine and continental	None	Intertidal
4. Cross-bedded sands and shales	Coarse sands > silts and shales	Predominate in south	Sands: large-scale cross-stratification. Silts & shales: laminated or rippled. Lignites and palaeosols.	Continental vertebrates & plant remains	Unimodal, northwards (off-shore)	Fluviatile
5. Calcareous sandstone channels	Coarse calcareous sandstones and sandy limestones	N-S trending shoe-strings	Channels, large-scale cross-stratification, quicksand structures	Mixed marine and continental	Bi-modal, major mode directed northwards (off-shore)	Estuarine channels

been found in bedded rock, it was quite different from the silicified wood of surface occurrence. The stratified wood is brittle and in small pieces, is largely or completely unsilicified, and if silicified the replacement is usually chalcedony or milky opal. We are definitely of the opinion that the vast majority of fossil wood found in the Sahara, including the Gebel Zelten area, is not contemporary with the sediments and represents a Pleistocene flora. From the artifacts and mammals distributed across the Sahara, we know that in Pleistocene times the climate included tropical and Savannah regimes. The development of laterites, caliches and silification are all in our mind associated with tropical, even monsoon conditions. The association of the three features can be seen in the Australian deserts today. Laterites and silicification are well known from the Deccan of India and from the Tertiary interbasaltic areas of Britain. In Gebel Zelten the wood is not sufficiently well preserved to permit specific identification, but dicotyledonous trees and palms are recognizable. All this wood however must be regarded as post-Miocene and therefore of no help in the palaeoenvironmental interpretation of the Zelten facies.

The majority of vertebrates are mammals, but there is also a representative selection of lower vertebrates. Fish remains are not infrequent, usually vertebrae and broken bones, with only occasionally teeth; sites 6405, 6416 and 6423 have

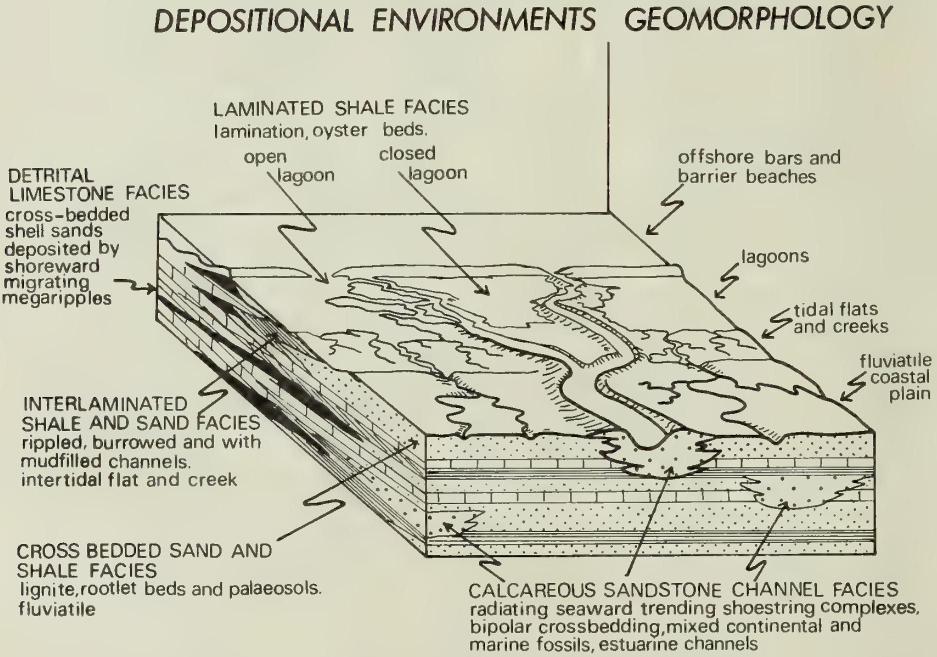
DEPOSITIONAL ENVIRONMENTS
GEOMORPHOLOGY
LAMINATED SHALE FACIES
lamination, oyster beds.
open lagoon
closed lagoon
DETRITAL LIMESTONE FACIES
cross-bedded shell sands deposited by shoreward migrating megaripples
offshore bars and barrier beaches
lagoons
tidal flats and creeks
fluviatile coastal plain
INTERLAMINATED SHALE AND SAND FACIES
rippled, burrowed and with mudfilled channels.
intertidal flat and creek
CROSS BEDDED SAND AND SHALE FACIES
lignite, rootlet beds and palaeosols.
fluviatile
CALCAREOUS SANDSTONE CHANNEL FACIES
radiating seaward trending shoestring complexes, bipolar crossbedding, mixed continental and marine fossils, estuarine channels

FIG. 2. Block diagram illustrating the supposed origin of the Miocene shore-line of the Sirte basin. (After Selley 1969, Text-fig. 17. Reproduced by courtesy of Dr R. C. Selley and the Geological Society of London.)

TABLE 2

Vertebrate Fauna of Gebel Zelten

Fish	
Elasmobranchii	*Odontaspis acutissima Agassiz*
	Carcharodon sp.
	Hemipristis serra Agassiz
	Pristis sp.
	Myliobatis sp.
Actinopterygii	*Lates* sp.
	Silurid
Reptiles	
Crocodylidae	*Tomistoma dowsoni* Fourtau
	Euthecodon sp.
	Crocodylus sp.
Chelonia	*Podocnemis aegyptica* Andrews
	Testudinid indet.
	Trionychid indet.
Birds	
Aepyornithidae	?*Eremopezus* sp.
Mammals	
Sirenia	gen. nov.
Proboscidea	*Mastodon angustidens* Cuvier
	Mastodon pygmaeus Arambourg
	Prodeinotherium hobleyi (Andrews)
Hyracoidea	Saghatheriine; cf. *Prohyrax*
Perissodactyla	
Rhinocerotidae	*Brachypotherium snowi* (Fourtau)
	Aceratherium sp.
Artiodactyla	
Anthracotheriidae	*Brachyodus* sp.
	Hyoboops africanus (Andrews)
	Hyoboops moneyi (Fourtau)
Suidae	*Diamantohyus africanus* Stromer
	Bunolistriodon massai Arambourg
	Bunolistriodon sp. nov.
	Listriodon sp. indet.
Giraffidae	*Zarafa zelteni* Hamilton
Sivatheriidae	*Prolibytherium magnieri* Arambourg
Tragulidae	*Dorcatherium libiensis* Hamilton
Palaeomerycidae	*Canthumeryx sirtensis* Hamilton
	Palaeomeryx sp.
	Palaeomerycid indet.
Bovidae	*Gazella* sp.
	Protragocerus sp.
	Eotragus sp.
Creodonta	
Hyaeondontidae	*Megistotherium osteothlastes* Savage
	Anasinopa sp.
Carnivora	
Canidae	*Afrocyon buroletti* Arambourg
	Amphicyonine indet.
Felidae	cf. *Metailurus*

yielded abundant fish; most of the identifiable remains from site 6416 are silurid. Amphibia are unknown and birds extremely rare; only three indubitable records stand. Arambourg's record (1961b) in the Gur el Menghil of an aepyornithid, and two ratite bones from sites 6404 and 6407. There are abundant and ubiquitous crocodile and chelonian remains, usually very fragmentary, with six taxa distinguishable. The profusion of large individuals of crocodiles suggests warm waters and plentiful food supply. The mammals are still being studied and the provisional list of species is to be found in the accompanying Table 2.

PRESERVATION

The majority of vertebrate remains are preserved in unconsolidated sands. Articulated skeletons are unknown and only a few partially associated skeletons are known. Relatively complete skulls, mandibles and bones are frequently found and show no signs of rolling or transport before burial. The preservation of bone is highly variable and three types of preservation are known, with sometimes gradations between. Bone found fully exposed on the surface is usually coated with desert varnish and well preserved, though the large temperature range causes the teeth to split and break up. Buried bone is usually similar to surface bone but without the varnish; it tends to be more brittle, but when carefully treated with bonding plastics can be readily recovered. A third category of bone is so brittle that it virtually disintegrates to dust on touching. Harris (1969) suggested two possible explanations for this phenomenon: a long period of weathering before burial and impregnation with salts in process of formation of subsurface salt layers.

ENVIRONMENT

From the sedimentary evidence of Gebel Zelten, Selley (1969) has established that a river system flowed northward across intertidal flats and compared the physical conditions to those of Texas coast and Trucial coast at present time. From the evidence of the shelly marine fauna, Doust (1968) has envisaged an environment most closely related to that of the tropical Atlantic. The evidence quoted by various authors on the basis of silicified wood is not accepted on grounds that the wood is not contemporary with the deposit. The aquatic vertebrates comprise fish, reptiles and a sea-cow. The fish are not abundant and mostly sharks and rays, implying marine or brackish waters. Crocodiles and turtles are ubiquitous, especially in the fluviatile facies; some of the crocodiles can be estimated to have been 8 metres long. Such large crocodiles and turtles would suggest tropical temperatures. Amongst the terrestrial mammals mastodon and *Deinotherium* were about equally abundant, with giraffes and anthracotheres as the dominant medium sized herbivores. Rhinoceroses and pigs were also present. Carnivores are rare, but include a gigantic hyaenodont. Interpretation of the vertebrate evidence suggests a forested belt along the river and savannah in the hinterland, similar to present day conditions along the banks of the Omo river as it flows into Lake Rudolf.

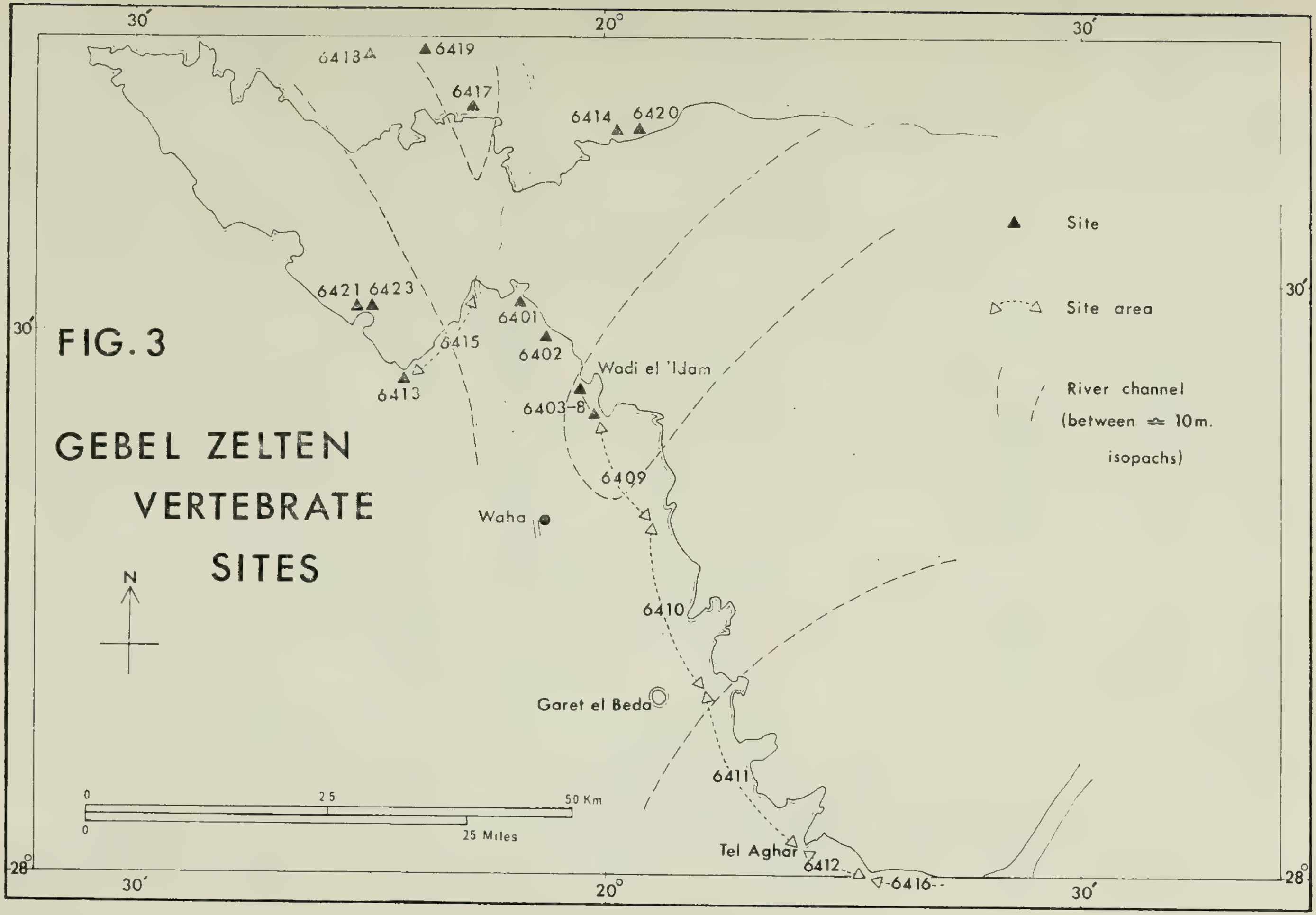

FIG. 3

GEBEL ZELTEN VERTEBRATE SITES

30′
20°
30′
30′
30′
28°
28°
30′
20°
30′
6413
6419
6417
6414
6420
6421
6423
6401
6402
6415
6413
Wadi el 'Idam
6403–8
6409
Waha
6410
Garet el Beda
6411
Tel Aghar
6412
6416
N
0
25
50 Km
0
25 Miles
▲ Site
Site area
River channel (between ≃ 10m. isopachs)

Fig. 3 shows the relationship of the palaeogeography to the distribution of the vertebrate sites. The sites vary in size and yield. There are no pockets of bone concentration; sites vary from 1 to 10 acres (0·5–5 Hectares) and the yield ranges from a few specimens to over a hundred. There are four groups of sites which have accounted for about 85% of the specimens; these are shown in Table 3 as groups I, III, V and VII. Bones are found throughout the succession, but there tend to be levels of concentration.

TABLE 3

Distribution of vertebrate stocks in Gebel Zelten

GROUP	I	II	III	IV	V	VI	VII
Sites	6417 6418	6420 6414	6421 6423	6401 6402	6403 6408	6409 6410	6412 6416
Coprolites	A	r	A	r	r	A	A
Fish	r	r	r	r	A	r	r
Chelonian	r	r	r	r	r	r	r
Crocodile	A	A	A	r	VA	A	A
Sirenian	VA	r	r				
Bird		r	r		r		r
Mastodon	A	A	A	r	A	A	VA
Deinothere	A	r	r	r	A	r	r
Rhinocerotid	r	r	VA	r	r	r	A
Anthracothere		r	r	r	r	A	VA
Suid		r	r	r	r	r	A
Giraffoid	r	r	r	r	VA	r	VA
Bovid		r	A	r	A	r	A
Carnivore		r	r		r	r	A

r = 1–10 specimens; A = 11–20 specimens; VA = more than 20 specimens.

These are found near the base of the succession in Group III sites, near the middle of the succession in Group V sites, and high in the succession in Group VII sites. In Group I sites fossils are found on the gravel plain. At sites in Group III and VII, fossils are found on the outwash from the gebel and may in some cases be redeposited there in recent times. Group I sites are on the intertidal flats; they have an abundance of sirenian remains, including three partial skeletons. Deinotheres are also surprisingly abundant, with three skulls found in close proximity at site 6418. Site 6417 has yielded only a few fragments. Group II sites are close to the northern face of the escarpment and in the outflow of estuarine channels. Some good individual specimens came from these sites, including a giraffid skull. Remains of 12 mastodon skulls were found in close proximity, but all were too weathered to collect. In Group III sites the species are varied and reasonably plentiful, but only rhinocerotids are very abundant. The sites fringe a major estuarine channel and represent accumulation on fluviatile banks and flood plains. The three sites in Group IV are within the estuarine channels and their yield is very low. In Group V are a series of sites grouped round an embayment in the gebel, which have a rich yield of many taxa, in particular giraffids. The wealth of bones in this area prompted the name Wadi el 'Idam. The sites in Group VI stretch for some 30 miles along the escarpment but have yielded relatively few specimens.

Group VII sites, occupy a stretch of escarpment about 11 miles long. Since bones all occur at a similar level high in the succession, there is no reason to further differentiate the sites. The fossil yield is enormous, almost as many specimens as found in groups III and V together. Deinotheres are the only terrestrial mammals which are not abundant, although the most complete mandible was found here. Mastodons, anthracotheres, and giraffes are all very abundant. The sites are the most remote from the sea; no marine fish or sirenians were recorded, and the region may represent fresh-water ponding beside which mammals frequently gathered. With the dying out of the gebel to the south nothing further can be traced.

AGE

All the evidence for dating the deposits is fairly consistent and taken together gives a reasonable result.

The Marada Formation at Marada rests on the Grier Bu Hascisc Formation, a marine sequence with *Nummulites intermedius fitcheli*, which is characteristic of Rupelian age in North African sequences. The Dor Zaggut sections of the Marada Formation contain shelly limestones with *Borelis melo* and *Borelis melo curdica*, the latter being characteristic of Burdigalian age in North Africa and the Middle East. Less reliable but consistent evidence comes from the shelly fauna, which Desio (1935) considered Burdigalian-Helvetian in Garet el Mazzala and slightly earlier, Aquitanian-Burdigalian in Gebel Zelten. The Marada Formation fauna is closely comparable with that of the Moghra Formation of Egypt (Said 1962).

The age evidence from the vertebrates must await detailed work on the mammals, but provisional estimates are possible. There are two regions where comparisons can be made, East Africa and France. While there are other sites with similar faunas, they are of no help in dating since they are only aged by comparison with western Europe or East Africa. The East African succession of Miocene mammals, mainly from sites around the north-east corner of Lake Victoria, comprises a sequence of faunas in tuffaceous deposits which have been radiometrically dated. Several species in the East African faunas are also found in Gebel Zelten; these include *Mastodon angustidens*, *Prodeinotherium hobleyi*, *Diamantohyus africanus*, *Hyoboops africanus*, *Brachyodus*, *Listriodon*, *Aceratherium* and *Brachypotherium*. This strong similarity at specific and generic level suggests near contemporaneity. The closest comparisons are with Karungu (Kisingiri) and Bukwa (Mt. Elgon), both of which sites have been dated around 22·5 million years, which equates with early Burdigalian (Bishop et al. 1969).

In France mammal faunas are to be found in or near type sections and the mammals from the Burdigalian in the Aquitaine basin include *Mastodon angustidens*, *Deinotherium cuvieri* (very similar to *Prodeinotherium hobleyi*), *Listriodon lockharti* and *Brachyodus onoideus*. *Mastodon* appears for the first time in mid Burdigalian sites and *Deinotherium* appears in late Burdigalian; these are the earliest records of proboscideans outside Africa. The close similarity of genera and species between France and Libya suggests closely comparable ages for the faunas. Allowing time for migration of species, it would be justifiable to suggest that the Gebel Zelten fauna is slightly earlier than the mid and late Burdigalian faunas of France, and so the conclusion that the Gebel Zelten fauna is early Burdigalian seems justifiable.

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INDEX TO VOLUME 22

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

Anatomical terms, etc., indicated *M.o.* refer to *Megistotherium osteothlastes* Savage (no. 7); those indicated *P.m.* refer to *Parabuchanosteus murrumbidgeensis* (White) (no. 5).

abducens nerve, *P.m.* 391
Acacia 98
Acarinina aspensis 452
    conicotruncata 455
    pseudotopilensis 463
    quetra 463
Aceratherium sp. 521, 525
Acetabularia 368–70
acetic acid development 379
Acicularia 369
Aciculella 368
Acodus 144, **162**
    curvatus **162**, 231; pl. 9, fig. 1
    erectus 162
    cf. *mutatus* 162
    unicostatus **162**, 231; pl. 9, figs. 2, 3
Acontiodus procerus 171
Actinolepis 393, 408
Actinopterygii 521
Aepyornithidae 521–2
Aestuarichthys fulcratus 257
Aetheodontidae 236, 347
Africa, fossil *Theropithecus* sites 5*
    Plio-Pleistocene baboons 1–123
Afrocyon buroletti 521
Ailuropoda 495, 507
Akidograptus acuminatus zone 130
Aldridge, R. J. 125–231
algae, calcareous 518
    green, Lower Palaeozoic of S. Scotland 355–76
Ambalodus 132, 144, **162–3**
    anapetus 138, 151, 157, 159, **163**, 229; pl. 3, fig. 4
    galerus 148, 157–8, **163**, 229; pl. 3, figs. 6, 8
    triangularis 157, 162, 229; pl. 3, fig. 7
    spp. **163**, 229; pl. 3, fig. 5
amorphognathoides zone, see *Pterospathodus*
Amorphognathus 132, 144, 148, 157, **163–4**, 167, 181
    ordovicica/us 163–4
    tenuis 127, 138, 143, 148, 151, 157, 159, **164**, 165, 228; pl. 2, figs. 3–4
Amphicentrum 319
Amphicyon shabazi 509
Amphicyonine, indet. 521
Anasinopa sp. 521
anastomosis, *P.m.* 388
Andrewsarchus 506
anterior dorso-lateral plate, *P.m.* 399–402, 406
anterior lateral plate, *P.m.* 401*, 406
Anthracotheriidae 521, 524–5
Anthracotherium ingens 508
aorta, dorsal, *P.m.* 390
Aphelognathus 144, **164–5**
    grandis 164
    siluricus 138, 151, 157, 160, **165**, 229; pl. 3, fig. 3
Applinella 472
    dumblei 471–2
apron, *P.m.* 402, 403*, 404, 406
Apsidognathus 144, 148, **165**, 167
    tuberculatus 141, 148, 158, **165**, 167–8, 228; pl. 2, figs. 7, 9
Apterodon 486, 508
Arabicodium 359
Arambourg, Professor C. 517
Aratrisporites 238
Arctolepida 407–8
armour, head and body, *P.m.*, restoration 409*
Arthrodires, buchanosteid, from Australia 377–417
Artiodactyla 521
astragalus, *M.o.* 487, 500*, **501**
Astrognathus 144, **165–6**
    tetractis 148, 157–8, 165, **166**, 228; pl. 3, fig. 1
Astropentagnathus 144, 148, **166–7**
    irregularis 148, 157–8, **166–7**, 228; pl. 2, fig. 5
atlas, *M.o.* 487, **499–500**, 499*
Atopocephala 239, **249–51**, 322–4, 347
    watsoni 249, **250–1**, 250*
Atractyliopsis 368
Aulacognathus 144, 148, 161*, **167–8**
    kuehni 148, 158, 160, **167–8**, 228; pl. 2, fig. 6
Australia, buchanosteid arthrodires of 377–419
Australian Museum, Sydney 379
Australopithecus 67, 114
autopalatine, *P.m.* 397–8

Baboons of African Plio-Pleistocene 1–123
Balclatchie, Ayrshire 367
Batophora 369
  oerstedii 376, 377*
Beaconia 251–2, 254, 347
  spinosa 264, 266
bear, brown, skull 503*; see *Ursus arctos*
Bekker's Kraal, South Africa 236–7
Bereich I conodont zone 132–3, 157; see *Icriodina irregularis* assemblage zone
Bereselleae 372
Birches Farm Lane, see Cowleigh Park
birds 521–2, 524
Birgeria 298, 330
Black Range Series (tuffs and rhyolites) 410*
Bloomfield Limestone 382, 410*, 412
Bobasatrania 319
body-plates, *P.m.* 381, 398–404, 407
Borelis melo 525
  melo curdica 525
Bornetella 363, 366, 369–71
  capitata 366–7
Boueira 359
Bovidae 521, 524
brachiopods, shelly facies zoning in Llandovery 128–9
Brachygnathopithecus 94
  peppercorni 96
Brachyodus onoideus 525
  sp. 521, 525
Brachypotherium 525
  snowi 521
Brachythoraci 380–1, 404, 407–8, 411
brain, *M.o.* **496–7**
  endocasts, 496*, 497*, 498*, 503
Breidden Hills 226
Broeckella 371
Brookvale, New South Wales 236–8
Brookvalia 239–40, 242–4, 249, **251–66**, 267, 269, 274, 291, 322–6, 347
  gracilis 236, 251, **252–9**, 253*, 260–4, 266, 286, 291, 327–31, 347
    fins, etc. 258–9, 329*
    growth of tail in 328–33, 329*, 348–9
    lower jaw 256–7, 256*
    palate 257–8
    pectoral girdle 254*, 258
    sensory canal system 257, 257*
    skull 254–6, 254*, 255*
    squamation 259, 263*
  latipennis 252, **262–4**
    scales 263*, 264
  parvisquamata 251–2, **259**, 347
  propennis 256, **259–62**, 261*, 291
    fins 260–1
    pectoral girdle 260
    skull 259–60
    squamation 262
  spinosa **264–6**, 265*, 291
    fins 266
    skull and pectoral girdle 264–6
    squamation 266
Brookvaliidae 236, **239–71**, 347
  classification and differences from Redfieldiidae 321–3
  snout 344*
Browne, Dr Ida 379
Bryantodus sp. 199
buccohypophysial canals, *P.m.* 388, 390
  foramina, *P.m.* 386, 390, 404
Buchan 381
buchanosteid arthrodires from Australia 377–419
Buchanosteidae 380, **381**
Buchanosteus 380–1, 383, 390–1, 396; see *Parabuchanosteus*
  murrumbidgeensis 379–81
  osseus 380
Bunolistriodon massai 521
  sp. nov. 521
Buttington Brick Works 135, 226

calcification in Dasycladaceans 372
Cameron, D. J. 383
Canberra, Australia 380
Canidae 521
canines, hyaenodontid 508*
Canthumeryx sirtensis 521
Carcharodon sp. 521
carotid arteries, *P.m.* 388, 390
  foramina, *P.m.* 386, 388
Carniodus 144, 151, **168–70**
  carinthiacus 153, **168**, 229; pl. 5, figs. 8–10
  carnicus 153, **168–9**, 229; pl. 5, fig. 11
  carnulus 153, 168, **169**, 170, 179, 196, 229; pl. 5, figs. 12–14
  carnus 153, **169–70**, 179, 196, 229; pl. 5, figs. 15, 16, 18
  cf. *eocarnicus* 170, 229; pl. 5, fig. 19
  spp. **170**
Carnivora 521, 524
carnivore, largest known 485
Catapsydrax dissimilis 447
  echinatus 447
Cavan Bluff limestone 410*, 412
Cavan Stage, limestones 383, 410*
celloni zone, see *Neospathognathoides*
Cercocebus 7, 14, 33*, 39*, 52, 55*, 92–4, 106
  albigena 6
  atys 7, 51*, 53*
  torquatus 88*
Cercopithecidae, Cercopithecinae 6, **94–7**
Cercopithecoidea 6
Cercopithecoides 101
Cercopithecus 7, 14, 33*, 55*, 92, 98 (footnote), 106–7
cerebral vein, anterior, *P.m.* 390
cervical articulation, *P.m.* 395, 404
Chaetangiacea 368
Cheirodopsis 338
Cheirolepis 341

- Chelonia 521–2, 524
- *Chiloguembelina* 426, 430, **431**
  - *goodwini* 430, **431**, 432; pl. 14, figs. 7, 8
  - *martini* 431, **432**; pl. 15, figs. 13–14
  - *parallela* 431
  - *venezuelana* 423–3
  - *wilcoxensis* 433
  - **woodi** 430, **432–3**; pl. 15, figs. 15–16
  - sp. 432
- Chiloguembelinidae 431–3
- *Chimaera* 388
- chimaeroides 388–9
- chlorite 365
- *Chlorocladus* 368
- Chlorophycaceae 358–67
- Chlorophyta 358
- *Cionichthys* 277, 322, 325, 347
- *Cladophlebis* 238
- *Clavigerinella* aff. *akersi* 473
  - *jarvisi* 473
- 'Cleithrolepidae' 336
- Cleithrolepididae 236, **302–15**, 335–7, 347
  - compared with Hydropessidae 335–7
  - relationships to Colobodontidae 338–42
- *Cleithrolepidina* **302–10**, 311–12, 321, 335–9, 341, 347
  - *extoni* **305–10**, 306*, 311–15, 336, 339, 341, 347
    - fins 310
    - pectoral girdle 307*, 310
    - skull 307–10, 307*, 308*, 340*
    - squamation 310
  - *minor* **303–5**, 309, 311–12, 335–6, 338
    - cheek region 303*, 304*, 304–5
- *Cleithrolepis* 302, **311–15**, 316, 320–1, 335–8, 347
  - *cuyana* **321**
  - *extoni* 305; see *Cleithrolepidina*
  - *granulata* 305, 307, 311, **312–15**, 313*, 336, 338, 341–2
    - fins 315
    - pectoral girdle 314*, 315
    - skull 313–15, 314*
    - squamation 315
  - *minor* 302–3, 311–12, 335–6
- *Climacograptus* aff. *reticularis* 138
  - sp. 138
- *Clorinda* 129
- *Clypeina* 369
- coccosteids, Upper Devonian of W. Australia 394*, 395
- coccosteomorphs 392–3, 399, 404, 406–7
- *Coccosteus* 395, 402, 406, 408
  - *osseus* 380, 390
- Codiacea 358–9
- Colobodontidae 236, **292–302**, 333–5, 347
  - hypothetical ancestry 333–5, 334*, 342
  - relationships with Cleithrolepididae 338–42
    - Hydropessidae 342–3
- *Colobodus* 333–5, 347
  - *koenigi* 333
- *Colobus* 14
- Conodont, gen. indet., sp. indet. A 147, **220**, 230; pl. 8, fig. 18
  - sp. indet. B 147, **220**, 230; pl. 5, fig. 29
- Conodonts, Llandovery, from Welsh Borderland 125–231
  - correlation, value in 132
    - W. Europe and N. America 153–6, 154*
  - facies control 158–9
  - faunal provincialism 156–8
  - faunas 143–60
  - homeomorphy 159–60
  - morphological terms 161*
  - previous research on Lower Silurian 132–4
  - stratigraphical distribution 143–51
  - techniques 134–5
  - zones 151–3
- coprolites 524
- *Costistricklandia* 128–9, 159
  - *lirata alpha* 141, 143; zone 131
    - *typica* 143; zone 131
- Cowleigh Park 141, 226–7
- Craighead Limestone, Caradocian 359, 362–3
- Craig-wen Quarry, Meifod 135
- cranio-spinal process, *P.m.* 393
- cranium, *M.o.* 487
- *Crassostrea gryphoides* 518
- Creodonta 521
- cribrosal areas, *P.m.* 396–7
- Crinoidal Limestone (of Taemas stage) 382, 410*, 413
- Crocodylidae 521–2, 524
- *Crocodylus* sp. 521
- *Crocuta* 497, 504–7
  - *crocuta* 504
- cucullaris depression, *P.m.* 393
- *Cucumeria* 518
- Currajong Limestone 410*
- Cyclocrineae 363–7
- *Cyclocrinites* 375
- cyclocrinitid algae, North American 375
- *Cylindroporella* 369
- *Cymopolia* 369, 371
  - *eochoristosporica* 369, 376, 377*
- *Cystograptus centrifugus* zone 128, 130
  - *vesiculosus* zone 130

- *Daedalichthys* **271–4**, 322–4, 327, 347
  - *higginsi* 272, **273–4**, 272*, 273*
- Damery Bridge 143, 226–7
- Dasycladacea 359–67
  - evolution, component factors of 370–2
  - patterns of reproductive structure 368–9
  - reproductive ontogeny 370
- Dasycladales 358, **360–7**, 368–72
  - evolution of reproductive structure in 358, 368–72
- *Dasycladus* 363, 368–70
- *Dasymys* 101
- *Dasyporella* 358, **362**

    norvegica 362
    cf. *norvegica* **362**; pl. 2, figs. 1–2
    silurica 362
Dasyporelleae 360–3
Dasyurodon 486
Daubentonia 115
Deinotherium 522, 524–5; see *Prodeinotherium*
    cuvieri 525
dentition of hyaenodonts 510
    of *M.o.* **497–8**, 506–7, 510
        functional analysis of 504–7
        measurements 502
dermal head-bones, *P.m.* 404; see also individual bones
Desio, Professor A. 516–7
Devonian, Lower 391
Diadelognathus 144, 157–8, **170–1**
    excertus 170–1
    nicolli 127, 143, 151, 153, **170–1**, 228; pl. 8, figs. 2–3
    primus **171**, 231; pl. 8, fig. 1
    n. sp. A of Nicholl & Rexroad 170
diagnosis of *M.o.* 487
Diamantohyus africanus 521, 525
Dicellograptus anceps 130
Dicellopygae 346
    draperi 274
    macrodentata 346, 346*
    tenuis 274
dicotyledonous trees 520
Dictyopleurichthys 251, 262, 347
    latipennis 252, 262–4; see *Brookvalia latipennis*
Dictyopyge decipiens 322
    macrura 291
'*Dictyopyge*' **290–1**
    illustrans **291**
    robusta **290**, 291
    symmetrica **290**, 290*, 291
Dictyosphaeria 358, 367
Dimorphosiphon 358–9
    rectangulare (*rectangularis*) **358–9**; pl. 1; pl. 2, figs. 4–5
Dingle 226–7
Dinichthys cf. *pustulosus* 386
Dinopithecus 93–4
    brumpti 66, 85–6
    ingens 70
Diplopora annulata 369
    a. annulata 376, 377*
    a. dolomitica 376, 377*
    pharenospongia 368
    tubispora 368, 376, 377*
Dipteronotus 335–7
    cyphus **321**
Distacodus 144, **171–2**
    incurvus 171
    obliquicostatus **171–2**, 231; pl. 9, fig. 4
Distomodus 144, 157–8, 161*, **172–5**
    ? *egregius* **172**, 173, 229; pl. 6, figs. 3, 4, 9
    ? *extrorsus* 157, **172–3**, 229; pl. 6, fig. 2
    kentuckeyensis 157, 172, **173**, 229; pl. 6, figs. 5–8, 11
    triangularis tenuirameus **173–4**, 229; pl. 6, fig. 13
        triangularis 151, 153, **174**, 229; pl. 6, fig. 12
    sp. nov. **171–5**, 229; pl. 6, fig. 10
Dolichothoraci 380–2, 404, 406–8, 411
Dollopterus 333–5, 347
Domas 226–7
Dorcatherium libiensis 521
dorso-lateral plate, *P.m.* 384
Doust, Dr H. 517
Drepanodus 144, **175–6**
    aduncus **175**, 231; pl. 9, fig. 17
    arcuatus 175
    suberectus **175–6**, 231; pl. 9, fig. 16
    spp. **176**, 231; pl. 9, figs. 14–15
Dunghan Formation 423–6, 428

ear region, *M.c.* **494–5**, 494*
Echinolampas 518
efferent hyoid artery, *P.m.* 391
elasmobranchs 389, 521
Elliott, G. F. 355–76
endocranial roof of coccosteids 394*
endocranium, *P.m.* 381–4, **385–98**, 391*, 406
endolymphatic(al) duct, *P.m.* 393, 395
Eocoelia 128–9, 159
    curtisi 141, 143; zone 131
    hemisphaerica 138; zone 131
    intermedia 138; zone 131
    sulcata zone 131
Eodasycladus ogilvae 369, 376, 377*
Eotragus sp. 521
epiotic prominences, *P.m.* 395, 406
? *Eremopezus* sp. 521
ethmoid, *M.o.* 493
Euarthrodira 381
Euleptaspis 380, 408
Eurythrocebus 14, 98–9, 107
Eusthenopteron foordi 258
Euthecodon sp. 521
evolution of Dasycladaceans, factors of 370–2
    reproductive structures in 368–72
evolutionary significance of Lower Palaeozoic green algae of S. Scotland 355–76
Exochognathus 144–5, **176–9**, 181, 211
    brassfieldensis 157–8, **176–7**, 178, 211, 230; pl. 7, fig. 4
    brevialatus **177**, 230; pl. 7, figs. 8–9
    caudatus **177–8**, 230; pl. 7, fig. 13
    detortus **178**, 230; pl. 7, figs. 7, 12
    keislognathoides 151, **178**, 230; pl. 7, fig. 5
    latialatus 151, 153, 170, **179**, 196, 230; pl. 7, figs. 10, 11
    sp. nov. 157, **179**, 230; pl. 7, fig. 6
extracapsular plate, *P.m.* 384
Exvotarisella 372

- eye-muscles, *P.m.* 391

- facialis nerve, *P.m.* 391
- Felidae 521
- fenestra, anterior, *P.m.* 396
    - exonarhina communis, *P.m.* 397
- fish 233–354, 377–419, 520–2, 524
- Foraminiferida 431–76
- Fronian 128, 130*, 131*
- frontal, *M.o.* **491**

- Game, P. M. 365
- garnets 365
- Garwood Collection 358
- *Gazella* sp. 521
- Gebel Zelten, Libya, geography 515, 516*
    - gigantic hyaenodont from Miocene 483–511
    - Miocene mammal faunas of 513–27
        - age 525–6
        - environment 522, 524
        - facies parameters 519
        - geology 517–8
        - palaeontology 518–22
        - preservation 522
        - sites 523*, 524
        - vertebrate fauna 521
- *Geitonichthys* **277–80**, 281, 322–3, 325, 347
    - *ornatus* **277–80**
        - fins 280
        - lower jaw 280
        - pectoral girdle 278*, 280
        - sensory canal system 280
        - skull 278–80, 278*
        - squamation 280
- *Gelada* 94
    - *rueppelli* 95
- Gelli Farm Quarry 136*, 226–7
- *Gemuendenaspis* 380, 408
- Ghazij Formation 423–6, 429
- *Gigantopithecus* 75, 114
- Gilberries Brook 135, 226–7
- Giraffidae 521, 524–5
- Girvan area 358
- *Girvanella* 358
- glenoid fossa, *P.m.* 384
- *Globanomalina ovalis* 476
- *Globigerapsis* 426, 430, **448**
    - *kugleri* 429, **448–9**; pl. 6, figs. 4–6; zone 449, 452–3
    - *mexicana* zone 431
    - *semiinvoluta* zone 431
    - *tropicalis* **449**; pl. 6, figs. 7–8
- *Globigerina* 426, 428–30, **433**, 468
    - *alanwoodi* 429, **433–4**; pl. 3, figs. 7–9
    - *angulata* 450
    - *angustiumbilicata* 430, **434**; pl. 1, figs. 1–3
    - *aquiensis* **434–5**; pl. 4, figs. 1–3
    - *aspensis* 452
    - *azerbaidjanica* **435**; pl. 2, figs. 1–3
    - **baylissi** 430, 435, **436**; pl. 2, figs. 4–6
    - *boweri* 437
    - *bulbosa* 436
    - *bulloides* 433, 436
    - *ciperoensis* 434, **437**; pl. 2, figs. 10–12
        - *angulisuturalis* 437
        - *angustiumbilicata* 434, 437
    - *colomi* 452
    - *concinna* 437
    - cf. *concinna* 437
    - *decepta* 443
    - *dissimilis* 447
    - *dubia lakiensis* 439
    - *eocaena* 468
    - *esnaensia* 457
    - *finlay* [sic] 444
    - *foliata* 438
    - *frontosa* **437–8**; pl. 1, figs. 22–4
    - *galavisi* 446
    - *globularis* 441
    - *haynesi* 428, **438**; pl. 4, figs. 7–9
    - *hornbrooki* 444
    - *inaequispira* 436, **438–9**; pl. 2, figs. 7–9
    - *incisa* 444
    - *irrorata* 459
    - *linaperta* **439**
        - *turgida* 445
    - *mckannai* 429, 434, **439**, 443; pl. 4, figs. 13–15
    - *nitida* 443
    - *nodosa* **440**; pl. 4, figs. 4–6
    - *officinalis* 430, 434, **440**, 441; pl. 1, figs. 7–9; zone Fig. 3, 427, 430–2, 434–5, 437, 439–40, 442, 447–8, 474–5
    - *ouachitaensis* 437, **440**; pl. 1, figs. 19–21
    - *palmerae* zone 443, 445
    - *parva* 440
    - *posttriloculinoides* 435
        - *clinata* **441**, pl. 1, figs. 13–15
    - *praebulloides leroyi* 430, 441–2; pl. 1, figs. 4–6
        - *occlusa* 430, 441, **442**; pl. 1, figs. 16–18
    - *prolata* **442–3**; pl. 1, figs. 10–12
    - cf. *prolata* 443
    - *pseudobulloides* 444, 461, 467
        - *varianta* 467
    - *pseudoeocaena* 438
    - *pseudoiota* 475
    - *pseudotriloba* 444
    - *quadranta* 462–3, 468
    - *rubra* 448
    - *soldadoensis* 429, **433**, 453; pl. 4, figs. 10–12
    - *spinuloinflata* 464
    - *spiralis* 434, 438
    - *stainforthi* 444
    - *topilensis* 471
    - *triangularis* **433–4**, 445; pl. 2, figs. 13–15
    - *trilocularis* 442
    - *triloculinoides* 428, **444**, 467–8; zone 461
    - *turgida* 429, **445**; pl. 3, figs. 4–6
    - *varianta* 467
    - *velascoensis* 428, **445**; pl. 3, figs. 10–12
    - *yeguaensis* **446**; pl. 3, figs. 1–3

Globigerinatheka 427, 430, **449**
  barri **449**; pl. 6, figs. 1–3
'Globigerinella' 475
Globigerinidae 433–49
Globigerininae 433–48
Globigerinita 426, 430, **446**
  africana **446**; pl. 5, figs. 7–9
  dissimilis **447**; pl. 5, figs. 10–12
  echinata **447**; pl. 5, figs. 4–6
  howei **448**; pl. 5, figs. 13–15
  naparimaensis 446
Globigerinoides 427, 430, **448**
  daubjergensis subzone 463
  higginsi 429, **448**; pl. 5, figs. 1–3
  'quadrilobatus' group 442
Globoquadrina primitiva 461
Globorotalia 426, 428, 430, **450**, 468, 475
  acuta 428, **450**; pl. 10, figs. 8–10
  aequa 428, **450**, 458, 463; pl. 10, figs, 1–4; zone Fig. 3, 427–9, 435, 439–40, 443–4, 450, 457, 459–60, 464, 466, 468–70
  albeari 453
  angulata 428, **450–1**, 456, 466; pl. 8, figs. 7–9; zone Fig. 3, 427–8, 444, 450–1, 455
  aragonensis 429, **451–2**; pl. 8, figs. 4–6; zone 429, 444–5
    twisselmanni 452
  aspensis 429, **452–3**, 454; pl. 15, figs. 10–12; *aspensis/esnaensis* zone Fig. 3, 427, 429, 439, 443, 452–4, 457, 459, 463, 468, 475–6
  broedermanni **453–4**; pl. 15, figs. 4–6
  caucasica 451
  centralis **454**; pl. 12, figs. 10–12
  cerroazulensis zone 431
  chapmani 428, **454–5**, 457, 462, 467; pl. 13, figs. 13–15
  collactea 442, 470
  compressa 455–6
  conicotruncata 428, **455**, 466; pl. 8, figs. 1–3; zone 466
  crassata 429, **455–6**, 465; pl. 11, figs. 7–9; *G. crassata/Truncorotaloides topilensis* zone Fig. 3, 427, 429–30, 432, 434–5, 437–43, 446–9, 454, 456, 459, 461, 464–5, 470–1, 473, 475–6
    aequa 450
    densa 464
  crassula 469
  ehrenbergi 428, **456–7**, 462; pl. 13, figs. 4–6
  elongata 466–7
  emilei 467
  esnaensis 429, **457**; pl. 15, figs. 7–9; zone see *aspensis*
  formosa[2] 429, **458**; pl. 9, figs. 1–3; zone Fig. 3, 427, 429, 434–5, 439–40, 443–5, 450, 452–4, 457–60, 463–4, 466, 468–70, 475–6
    gracilis 429, **458**; pl. 11, figs. 4–6
  haunsbergensis 457
  inconspicua[2] zone 461
  irrorata **458–9**; pl. 14, figs. 4–6
  lehneri 430, **459**, 464; pl. 14, figs. 12–14; zone 430, 447
  marginodentata 428–9, 456, **460**; pl. 11, figs. 1–3
  mattseensis 453
  membranacea 456–7
  nagappai 459
  occlusa 428, **460**; pl. 10, figs. 11–13
  palmerae zone 453, 459
  parva 428, **460**; pl. 9, figs. 4–6
  aff. *primitiva* **461**; pl. 14, figs. 9–11
  pseudobulloides 428, **461–2**, 463, 468; pl. 12, figs. 1–3
  pseudomenardii 428, 457, **462**, 466; pl. 13, figs. 7–9; zone 428, 467
  pusilla[2] zone 428, 444, 457, 466
  quadrata 457–8, **462–3**, 468; pl. 12, figs. 4–6
  quetra **463–4**; pl. 10, figs. 5–7
  renzi **464**; pl. 13, figs. 10–12
  rex 456, 465; zone 429, 431, 459, 465
  simulatilis 466
  spinuloinflata 430, **464**
  spinulosa 459, **465**; pl. 14, figs. 1–3
  subbotinae 428–9, **465–6**; pl. 10, figs. 14–16
  tadjikistanensis 428, **466**; pl. 8, figs. 10–12; zone 466
  triplex 461
  troelseni 428, **466–7**; pl. 13, figs. 1–3
  uncinata subzone 444, 450
  varianta **467–8**; pl. 12, figs. 7–9
  velascoensis 428, 451, **468–9**; pl. 9, figs. 7–9; zone Fig. 3, 427–8, 435, 438–9, 443–5, 450–1, 455, 457, 459–60, 462–3, 466–9
    parva 460
  whitei 463, **469**, 470; pl. 15, figs. 1–3
  wilcoxensis 428, 463, **469–70**
    acuta 450
Globorotalias, *Rotalia*-like, zone of 468
Globorotaliidae 450–71
Globorotaloides turgida 445
glossopharangeal nerve, *P.m.* 391
Glossopteris 238
Glyptograptus persculptus zone 128, 130
Glyptolepis 388
Gonatodus 346
Goniolinopsis 368
Goodradigbee River 380
Gorgopithecus 10, 93–4, 101
  darti 96
  wellsi 85, 96
Gorilla 29, 32, 36, 38, 41, 43, 74, 104, 112
Gosford, New South Wales 237–8
Gothodus 145, 160, **179–80**
  communis 180
  costulatus 179–80
  ? sp. nov. **180**, 229; pl. 6, fig. 1
Graig-wen Quarry 226–7
graptolite zones, Llandovery 128, 130*
Gray, Mrs Robert, collection 358

Guembelina [*Gümbelina*] *goodwini* 431
  martini 432
  midwayensis 431
Gullet Quarry 134, 141, 142*, 226–7

Hadrognathus 145, **180–1**
  staurognathoides 138, 141, 148, 151, 153, 155, **180–1**, 228; pl. 2, figs. 8, 10, 11
    assemblage zone 151–3, 152*, 155
Hadropithecus 114
Halicoryne 369
Halimeda 358–9
Hamilton, W. R. 513–27
Hantkenina 427, 430, **471**
  alabamensis 471
  aragonensis 452, 471–3; zone 443, 453
  dumblei **471–3**; pl. 7, fig. 18
  lehneri 473
  longispina 472
  mexicana 472, **473**; pl. 7, figs. 16–17
    aragonensis 473
Hantkeninidae 471–6
Haplolepis 298
Harris, Dr J. M. 517
Hastigerina danvillensis 474
Haugh Wood 143, 226–7
Hawkesbury group 237–8
head-shields, *P.m.* 382
Heightingtonaspis anglica 408
Helichthys 271, **274–7**, 322–4, 347
  browni 274–5
  ctenipteryx 274
  draperi 274
  elegans 274, **275–7**, 275*, 276*
  grandipennis 274
  obesus 274
  stegopyge 274
  tenuis 274
Hemipristis serra 521
Hemipsalodon 486
Hibbardella 145, 161*, **181–2**
  angulata 181
  ? *prima* **181**, 230; pl. 6, fig. 16
  ? *trichonodelloides* **182**, 230; pl. 6, figs. 17–18
  sp. nov. **182**, 231; pl. 6, figs. 14–15
Hillend Farm, 138, 140*, 226
Hindeodella 145, **182–3**, 190
  confluens 208, 216, 219
  equidentata **182–3**, 230; pl. 8, fig. 19
  excavata 183, 194, 201, 207, 213, 218
  subtilis 182
  n. sp. of Walliser 189
Hippopotamus 101
Hollybush Quarry 134, 141, 226–7
Holonema 397, 401
holotype of *M.o.* 487
Homo sapiens 83
  Acheulian 100
Hopefield 5, 5*, 70, 73, 73*
Hope Valley, Salop. 135, 138, 139*, 226–7
humerus, *M.o.* 487, **500**, 500*, 503
Hutchinson, P. 233–354
Hyaena sp. indet. 507
hyaena, skull 503*; see *Crocuta crocuta*
Hyaenaelurus fourtaui 507–8
Hyaenodon 486, 493, 496, 499
  mustelinus 505, 507
hyaenodont, gigantic, Miocene of Libya 483–511
Hyaenodontidae **485–6**, 521
Hyaenodontinae **486**
Hyainailourinae 486
Hyainailouros 486, 507–9
  bugtiensis 509–10
  fourtaui 507–8, 510
  grandis 509
  lahiri 509
  nyanzae 509–10
  sulzeri 507–10
Hydrolagus 388
Hydropessidae 236, **316–21**, 347
  compared with Cleithrolepididae 335–7
  relationships with Colobodontidae 342–3
Hydropessum 236, **316–21**, 335–8, 342–3, 347
  kannemeyeri **316–21**, 317*
    fins 319–20
    pectoral girdle 318*, 319
    skull 317–9, 318*, 320*
    squamation 320–1
Hyoboops africanus 521, 525
  moneyi 521
hyoid vein, *P.m.* 393
hyomandibula, *P.m.* 391
hyomandibular nerve, *P.m.* 392
hypodigm of *M.o.* 487
hypophysial fenestra, *P.m.* 386, 389
  fossa, *P.m.* 386, 388, 406
  stalk, *P.m.* 389
Hyracoidea 521

Ichthyokentema purbeckensis 345
Icriodella 128, 133–4, 145, 148, 153, 155–7, 160, **183–6**, 187, 221
  deflecta 127, 135, 138, 143, 148, 149*, 151, 155, 157, 159, **183–4**, 185, 228; pl. 1, figs. 4–7; see *discreta–deflecta* assemblage zone
  discreta 135, 148, 149*, 151, 155, 157, 159, **184**, 228; pl. 1, figs. 1–3
  discreta–deflecta assemblage zone 151, 152*, 155, 159
  inconstans 127, 138, 141, 143, 148, 149*, 153, 158–9, **184–5**, 186, 228; pl. 1, figs. 13–17
    assemblage zone 151–3, 152*, 155–6, 159
  malvernensis 127, 141, 143, 148, 149*, 153, 158, 159, 184, **185–6**, 228; pl. 1, figs. 8–12
  cf. *malvernensis* 141, 148, 149*, 186, 228
  superba 183–4
  n. sp. of Pollock *et al.* 183
Icriodina 133–4, 145, 148, 155–7, **186–7**

    irregularis 132–3, 148, 149*, 157, **186–7**, 228; pl. 2, fig. 1
        assemblage zone 128, 133–5, 138, 151, 155–6; see Bereich I
    stenolophata 133, 148, 158, 187
    sp. 149*, **187**, 228; pl. 2, fig. 2
Idmonea fenestrata 518
Idwian 128, 130*, 131*
Inopinatella 372
infranuchal pits, *P.m.* 395
    ridge, median, *P.m.* 395
interlateral plate, *P.m.* 402, 403*, 405*, 406
Intermurella 358, **361–2**, 363, 371
    scotica 361–2; pl. 3, fig. 3; pl. 4
internasal wall, *P.m.* 397
irregularis zone, see *Icriodina*
Ischadites 358, 365, **367**
    sp. **367**; pl. 2, fig. 3; pl. 10
Ischnognathus 486
Ischnolepis 236–7, **239–49**, 322–6, 328, 347
    bancrofti 237, **240–9**, 241*
        fins 247–9, 248*
        lower jaw 244, 245*
        palate 246–7
        pectoral girdle 246*, 247
        skull 240–4, 242*, 243*
        squamation 249

jaw, *M.o.*, functional analysis of 504–6, 505*
JOLLY, C. J. 1–123
jugal, *M.o.* **490**
jugular canal, *P.m.* 392
    vein, *P.m.* 392–3

Kaiso 5, 5*, 67, 72, 73*
Kanjera 5*, 6, 8–43, 71, 73*
Keislognathus ? n. sp. of Rexroad 178
Khirthar Formation 423–6, 429–30
Kockelella patula 160; zone 201
Koninckopora 365
Koobi Fora 5, 73
Kujdanowiaspis 390–3, 395, 397–8, 404, 406
    anglica 408

labyrinth area, *P.m.* 393
lacrymal, *M.o.* 490
Lacrymorphus perplexus 367
Lasalichthys 322, 347
lateral plates, *P.m.* 402
Lates sp. 521
Lawnia taylorensis 345
Leakitherium 486
Lepisosteus 330
Leptaspis 408
levator muscles of head, *P.m.* 395
    palatoquadrati, *P.m.* 390
Libypithecus 92
'*Ligondina*', see *Ligonodina*
Ligonodina 145, **187–90**
    egregia 172
    ? *extrorsa* 172
    ingens 189
    kentuckyensis **188**, 189, 230; pl. 8, figs. 15–16
    pectinata 187
    petila **188**, 230; pl. 8, fig. 11
    salopia **188–9**, 230; pl. 8, fig. 17
    silurica 157, 188, **189**, 230; pl. 8, figs. 10, 13
    ? *variabilis* **189–90**, 230; pl. 8, fig. 14
Limnocyoninae, Limnocyontidae 486
Lingula 129, 159
Linley, see Norbury
lion, skull 503*; see *Panthera leo*
Listriodon 521, 525
    lockharti 525
Llandeilo 226
Llandovery 128, 226–7
Llandovery Series, conodonts from Welsh borderland 125–231
        not in type area 135
    correlation of conodont zones 154*
    outcrop in Wales and Welsh borderland 129*
    zones 130*, 131*
Llansantffraid ym Mechain, see Montgomeryshire, Gelli Farm Quarry
Lonchodina 145–6, **190–3**
    cristagalli 193
    detorta 153, **190**, 230; pl. 8, fig. 6
    elegans 190
    fluegeli 153, 155, **190–1**, 230; pl. 8, fig. 7
    greilingi **191**, 219, 230; pl. 8, fig. 4
    typicalis 190
    walliseri **191–2**, 230; pl. 8, fig. 5
    sp. A **192**, 230; pl. 8, fig. 9
    sp. B **192**, 230; pl. 8, fig. 8
    sp. C **192–3**, 230; pl. 8, fig. 12
    ? sp. of Rexroad 192
    n. sp. (a) of Walliser 190
    n. sp. (b) of Walliser 191
Long Mynd 138, 226
Lothagam 5, 5*, 73*
Lunsempfwa Valley, Zambia 237

Macaca 6–10, 12, 14, 18, 31, 33*, 38, 39*, 46, 55*, 106
    gelada 93, 95
    nemestrina 6, 12, 107
Machaeroidinae 486
Machairodus incurvus 171
Macroporella 371
Maesopsis (food of baboons) 98
Magnier, M. 517
magnum, *M.o.* 487, 501*
Majurgong Stage 410*
Makapan 5, 5*, 67–9, 72–3, 73*
Malvern Hills 141, 143, 226
    West 141, 226–7
mammal faunas, Miocene, of Gebel Zelten 513–27, **521**

Mandrillus 6–10, 12, 14, 21–2, 31, 33*, 35, 38–9, 39*, 42, 46, 49, 51–2, 55*, 57–8, 60–1, 90, 92–4, 102*, 103*, 104, 106–8, 114
    leucophaeus 51*, 91*, 107*, 108*; pl. 1, figs. a, b
    sphinx 7, 53*, 74–6, 75*, 105, 109
Manlietta **297–301**, 333–5, 347
    crassa 297, **298–301**, 298*, 333
        fins 301
        lower jaw 301
        skull 299–301, 299*, 300*
        squamation 301
Marshbrook outlier 138, 226–7
Mastodon 522, 524–5
    angustidens 506, 521, 525
    pygmaeus 506, 521
Mastopora 358, **363–7**, 368, 370–2, 375
    fava 358, 364, **366–7**, 368; pl. 7, fig. 3; pl. 8, fig. 4; pl. 9
    parva 358, **364–6**, 367, 372; pl. 5, fig. 3; pl. 7, figs. 1, 2; pl. 8, figs. 1–3
    pyritiformis 365
maxilla, *M.o.* 487, **490**
median dorsal plate, *P.m.* 399, 400*, 406
Megistotherium 483–511 *passim*, **486–7**
    osteothlastes **487–502**, 488–501*, 503*, 505*, 521; plates 1–4; see also individual bones, etc. (indicated *M.o.*)
        other material comparable with 507–10
        prey of 506
Meidiichthys **292–5**, 333–5, 339, 343, 347
    browni **293–5**, 293*, 294*, 333, 339, 340*
melobesioids 368
Mendocinia 296–301, 333–5, 347
    brevis 299
Meridensia 333–5
cf. *Metailurus* 521
metapodial, *M.o.* 487, **501**, 501*
Metapterodon 486
Middletown 135, 226–7
Migmatocephala 379–80, **381**
Minsterley Lane 226–7
Mizzia 371
Molybdichthys 277, 279, **280–5**, 322–3, 347
    junior **281–5**, 282*
        fins 284–5
        lower jaw 283–4
        pectoral girdle 283*, 284
        skull 281–3, 283*, 284*
        squamation 285
Monoclimacis crenulata zone 130
    cf. *crenulata* 132
    greistonensis zone 128, 130, 141, 153
Monograptus becki 138
    convolutus zone 130, 138
    crispus zone 130
    cyphus 133
    halli 138
    sedgwickii zone 130, 133
    turriculatus zone 130, 138, 151
Montgomeryshire 135, 226
Murrumbidgee River 380
Murrumbidgee Series, Lower Devonian of Australia 380, 383, 410*
musculus adductor mandibulae, P.m. 391
    constrictor dorsalis, P.m. 390
        hyoideus, P.m. 391
    externus posterior, P.m. 391
Myliobatis sp. 521
myodomes, *P.m.* 391–2
Myrica integerrima 518

Narrabeen group 237–8
nasal, *M.o.* **490**
naso-maxillary vein canal, *P.m.* 388, 390
Nematoptychius greenocki 256
Neomeris 369
    stipitata 365
Neoprioniodus 146, **193–6**
    bicurvatus 216
    ? cf. *brevirameus* 172
    conjunctus 193
    costatus[2] 151, 153, **193**, 194, 230; pl. 5, fig. 22
        paucidentatus **193–4**, 229; pl. 5, figs. 20–1
    excavatus **194**, 230; pl. 5, fig. 25
    latidentatus **194–5**, 230; pl. 5, fig. 24
    multiformis **195**, 230; pl. 5, fig. 26
    planus 157, **195**, 230; pl. 5, fig. 23
    subcarnulus 195
    subcarnus 151, 153, 170, 179, **195–6**, 230; pl. 5, fig. 17
    triangularis tenuirameus 173
        triangularis 174
Neospathognathodus 133, 146, 148, 155–6, **196–8**
    bullatus 141, 148, 157–8, **196**, 197, 228; pl. 3, fig. 15
    celloni 132–4, 141, 148, 153, 156, 158, 160, 165, **197**, 228; pl. 3, figs. 9–12
        assemblage zone 132–4, 155–8
    ceratoides 157
    latus 157
    pennatus 133, 141, 148, 153, **197**, 198, 228; pl. 3, figs. 13, 16
    sp. **198**, 228; pl. 3, fig. 14
neurocranial cavity, *P.m.* 396, 406
neurocranium, *P.m.* 404, 406
New House, Marshbrook 226–7
New South Wales Triassic fishes 233–354
Nonion danvillensis 474
    micrus 474
    wilcoxensis 476
Norbury 135, 226–7
Norway, Ordovician of 359
nostrils, *P.m.* 397
Novantiella 358, **362–3**
    ordoviciana **362–3**; pl. 6
nuchal, *P.m.* 383–4, 404

- nuclei, small, migration of, in Dasycladaceans 371–2
- *Nummulites intermedius fitcheli* 525

- occipital, *M.o.* **492**
- oculomotor nerve, *P.m.* 391–2
- *Odontaspis acutissima* 521
- *Oistodus suberectus* 175
- Olduvai 5, 5*, 6, 54–66, 71, 73*
  - Bed IV series 64–6
  - Upper bed II series 54–63
  - Bed I and Lower bed II series 63–4
- Olorgesailie 5, 5*, 6, 43–54, 71, 73*
- Omo 5, 5*, 66, 72, 73*
- Onny River 135, 226–7
- orbito-ethmoid 'slit', *P.m.* 397
- orbits, *P.m.* 381, 404, 407
- Orbulininae 448–9
- *Orbulinoides beckmanni* zone 430, 446, 449, 464
- Oxyaenidae 506
- *Ozarkodina* 146, 161*, **198–202**
  - *adiutricis* 132, 155, **198**, 200, 229; pl. 5, figs. 2–3
  - **alisonae** 127, 143, 151, 153, 158, **198–9**, 228; pl. 5, figs. 4, 6
  - *edithae* 199, 200
  - cf. *edithae* 160, **199–200**, 229; pl. 4, fig. 17
  - *gaertneri* 132, 143, 151, 153, 156, **200**, 229; pl. 5, figs. 5, 7
  - *hanoverensis* 157, **200–1**, 229; pl. 5, fig. 1
  - *jaegeri* 199
  - *media* **201**, 229; pl. 4, fig. 21
  - *typica* 160, 198–9, **201–2**, 229; pl. 4, figs. 18–20
  - sp. of Rhodes 201
  - n. sp. A of Pollock *et al.* 214
  - n. sp. B of Pollock *et al.* 214

- Pab Formation 424
- pachyosteomorphs 399, 408, 411
- Palaeomerycidae, sp. indet. 521
- *Palaeomeryx* sp. 521
- palaeoniscoid body lobe, squamation of 328–33, 349
- Palaeozoic, Lower, S. Scottish green algae 355–76
- palatine, *M.o.* **490–1**
- palatoquadrate, *P.m.* 396*, 398, 406
- palms 520
- *Paltodus* 146, 161*, **202–3**
  - *acostatus* 162, 204–5
  - *costulatus* **202**, 231; pl. 9, fig. 21
  - *debolti* **202–3**, 231; pl. 9, fig. 18
  - *dyscritus* **203**, 231; pl. 9, fig. 19
  - *gracilis* 203
  - *migratus* **203**, 231; pl. 9, fig. 20
  - *simplex* 204
  - *staufferi* 205
  - *subaequalis* 202
  - *unicostatus* 202–3, 205–6
- *Pan* 29, 31, 36, 38, 41, 43
- *Panderodus* 143, 146–7, **203–7**
  - *denticulatus* 204
  - cf. *gracilis* 160, **203–4**, 231; pl. 9, figs. 12–13
  - *robustus* 207
  - *serratus* **204**, 231; pl. 9, fig. 7
  - *simplex* **204–5**, 231; pl. 9, figs. 8, 9
    - assemblage zone 134
  - cf. *staufferi* 160, **205**, 231; pl. 9, fig. 10
  - *unicostatus* 143, 203–4, **205–6**, 231; pl. 9, figs. 5–6
    - *serratus* 204
    - *unicostatus* 206
  - sp. A **206–7**, 231; pl. 9, fig. 11
- *Panthera* 504
  - *leo* 504, 507
  - *tigris* 504, 507
- *Papio* 6–10, 12, 14, 17–18, 21–2, 33*, 35, 37, 39, 39*, 42, 46, 49, 51–2, 54*, 55*, 57–8, 60, 74, 77–82, 80*, 84, 87–90, 89*, 92–4, 98–9, 101–9, 102*, 103*, 112–4, 116
  - *anubis* 29, 32, 36, 38, 41, 43, 53*, 54, 74, 88*, 91*, 107*, 108*
    - *neumanni* 74–6, 75*
  - *cynocephalus* 7, 54
    - *kindae* 47*, 48*, 79; pl. 2, figs. a, b
  - *darti* 85, 96
  - *gelada* 95
  - *ursinus* 47*, 48*, 79, 112; pl. 2, figs. c, d
  - (*Simopithecus*) *serengetensis* 5–6, 84–5
- Papionini 94–7
- **Parabuchanosteus** 379–80, **381**, 382–414
  - *murrumbidgeensis* 379–81, **382–404**, 405–14 *passim*, 382*, 384*, 385*, 387*, 389*, 391*, 394*, 396*, 398*, 400*, 401*, 403*, 405*, 409*
    - anatomical features, etc., see under individual names (indicated *P.m.*)
    - characters 404–7
    - localities of 380, 411–4
    - relationships 407–11
- *Paracentrophorus madagascariensis* 345
- *Paramesolepis* 338
  - *tuberculata* 331, 332*
- paranuchal plate, *P.m.* 383–4, 399
- *Parapapio* 6, 84–5, 92–3, 101
- parasphenoid, *P.m.* 381, 385–6, 387*, 388–90, 404, 406
- parietal, *M.o.* **491–2**
- *Patriofelis* 494, 504
- pectoral fin, *P.m.* 406
- *Pelomys* 101
- *Pentameroides* 129, 131, 159
- *Pentamerus* 129, 131, 159
- perichondral bone, *P.m.* 393
- Perissodactyla 521
- perleidiform fishes, Triassic of South Africa and New South Wales 233–354
- Perleidiformes 236–7, **292–321**, 347
  - classification 333–7
  - evolution 338–43
  - families, relationships between 348*

  genera provisionally ascribed to 321
  origins 343–7
Perleidus 267, 293, 333–5, 341, 347
  piveteaui 295, 341
Permopora keenae 365
petalichthyids 393
Phacochoerus 113–4
phlyctaenaspids 408
Phlyctaenichthys **267–71**, 322–3, 325, 347
  pectinatus 267, 267*, **269–71**
    fins 270–1
    lower jaw 270
    pectoral girdle 268*, 270
    skull 268*, 269–70, 270*
    squamation 271
Pholidophorus browni 293
  falcifer 333
pholidosteid, *P.m.* 393
Pholidosteus 388, 395, 404, 406
Phyllotheca 238
pineal bone, *P.m.* 396
pituitary, *P.m.* 388, 390
  sinus 390–1, 406
  vein 392
planktonic foraminifera from Rakhi Nala 421–82
  distributions Figs. 1–3 (following 426)
  zones 423, 427–31
Planulina membranacea 456
Platysomus 338–9
Plectospathodus 147, 191, **207–8**
  elegans 208
  extensus **207**, 218, 230; pl. 7, figs. 21–2
  flexuosus 157, 207, **208**, 230; pl. 7, fig. 24
  irregularis 157, **208**, 230; pl. 7, fig. 23
Plesiadapis 115
Plourdosteus 404
Plowden 138, 140*, 226–7
Podocremis aegyptica 521
Polypterus 327
Porticulasphaera mexicana zone 430
postcranial skeleton, *M.o.* 485, **499–501**
  measurements 502
posterior dorso-lateral plate, *P.m.* 402, 406
posterior postorbital process, *P.m.* 393, 406
postmarginal plate, *P.m.* 383–4
post-nasal bone, *P.m.* 396
postorbital plate, *P.m.* 383, 390
  processes, *P.m.* 391–2
post-suborbital line, *P.m.* 397
Powys Castle Formation 135
premaxilla, *M.o.* 487, **490**
preorbital plates, *P.m.* 381, 383–4, 404
pre-rostral bone, *P.m.* 396
Presbytis entellus 7
Prioniodella inclinata 213
Prioniodina bicurvata 194, 216
    pronoides 216
  excavata 194–5
  irregularis 208
  tropa 216
Prioniodus angulatus 181
  bicurvatus 216
  conjunctus 193
  excavatus 194
Pristiograptus cyphus zone 130
  gregarius zone 130
Pristis sp. 521
Pristisomus 333
Proboscidea 521
Procheirichthys **295–7**, 333–5, 341, 347
  ferox **295–7**, 296*
    fins 297
    pectoral girdle 297
    skull 295–6, 340*
    squamation 297
Procynocephalus 92–3
Prodeinotherium hobleyi 506, 521, 525
Prohyrax 521
Prolibytherium magnieri 521
Propterodon 486
Protragocerus sp. 521
Proviverrinae, Proviverrini 486
Pseudobeaconia bracaccinii **292**
  elegans **292**
pseudobranchial artery, efferent, *P.m.* 391
  canal, *P.m.* 392
Pseudogloborotalia aragonensis 451
  broedermanni 453
  quetra 463
Pseudohastigerina 426, 429–30, 455, **474**, 475
  danvillensis **474**; pl. 7, figs. 7–8
  eocenica 476
  iota 474–5
  micra **474–5**; pl. 7, figs. 11–12
  pseudoiota **475**, 476; pl. 7, figs. 3–4
  sharkriverensis 475–6; pl. 7, figs. 1, 2, 5, 6
  wilcoxensis 475–6
  aff. *wilcoxensis* **476**; pl. 7, figs. 9–10
Pterodon 486, 496, 498, 505, 509
  africanus 508
  grandis 509
  nyanzae 508–9
  sp. 509
Pteronisculus 244, 246–7, 341
  stensioei 332, 332*
Pterospathodus 147–8, **208–9**
  amorphognathoides 132–3, 141, 143, 148, 153, 156, 197, **208–9**, 228; pl. 3, figs. 17–19
    assemblage zone 132–4, 151–3, 152*, 156, 158
Pterospathodus amorphognathoides–Spathognathodus ranuliformis assemblage zone 133–4, 156–8
Pulvinulina crassata 455
  menardii 450
  velascoensis 468
Pygodus 147, 160, **209–10**
  anserinus 209
  ? *lyra* 148, 157–8, **210**, 229; pl. 3, fig. 2
Pygopterus nielseni 332*, 333

Rachendachhypophyse, *P.m.* 388–9
Rakhi Nala, Palaeocene–Eocene succession 424, 425*
  planktonic foraminifera from 421–82
Ranikot Formation 423–5
Ratites 522
Receptaculitacea 367
Receptaculitales **367**
Receptaculites Limestone 410*, 412–3
rectus externus muscles, *P.m.* 392
redfieldiform fishes, Triassic, of South Africa and New South Wales 233–354
Redfieldiiformes 236–7, **238–92**, 347
  classification 321–5
  families, relationships between 348*
  feeding 326–8
  genera provisionally ascribed to 289–92
  gill ventilation 326
  origin of 343–5
  skull, functional analysis of 325–8, 348
  snout, evolution of 344*
  un-named forms possibly Redfieldiiformes 292
Redfieldiidae 236, **271–85**, 347
  classification and differences from Brookvaliidae 321–3
  snout 344*
Redfieldius 277, 322, 327, 347
reproductive structures in Dasycladales, evolution of 368–72
reptiles 521–2
rhino-capsular bones, *P.m.* 383
Rhinocerotidae 521, 524
Rhuddanian 128, 130*, 131*, 135
Rhynchognathodus ? n. sp. of Rexroad 157, 179
rostral bone, *P.m.* 396
  capsule, *P.m.* 383
Rostricellula 129, 159
rostro-pineal bone, *P.m.* 381, 384, 389*, 359–7, 404
Roundya 181
  brevialata 177
  caudata 177
  detorta 178
  latialata 179
  ? *prima* 181
  ? *trichonodelloides* 181
  truncialata 177
Rudolf, Lake, sites 5*, 73*
Rushlandia gilli **292**

saghatheriine cf. *Prohyrax* 521
Sagittodontus 147, **210–1**
  edentatus 157–8, **210–1**, 218, 230; pl. 7, figs. 1–3
  robustus 157, 210–1
St Peter's, New South Wales 237
Sakamenichthys germaini **289**
Samanta, B. K. 421–82
Sarkastodon 506
Savage, R. J. G. 483–511
  & Hamilton, W. R. 513–27
Sawdde Gorge, Llandeilo 135, 226–7
scapulo-coracoid, *P.m.* 403*, 404, 405*, 406
Schizoneura 238
Schizurichthyidae 236, **285–9**, 323–4, 347
Schizurichthys **285–9**, 323–4, 326, 347
  pulcher **285–9**, 287*, 323
    fins 286–8
    pectoral girdle 286
    skull 286, 288*
    squamation 288–9, 289*
Scotland, southern, Lower Palaeozoic green algae from 355–76
Scyphiodus 133
selachians 390
Selley, Dr R. C. 517
sensory canal system, *P.m.* 381, 384, 404
Sheinton Brook 141, 226–7
shoulder-girdle, *P.m.* 404
Shropshire, south, Llandovery outcrops 137*; see also Long Mynd
Siegenian–Emsian Stage 382, 407
silurid fishes 521–2
Simopithecus 1–123 *passim*, **95–7**; see also *Theropithecus*
  danieli 85, 96–7
  darti 69, 85–6, 96
  jonathani 64–5, 64*, 82, 85–6, 89*, 95–6
  leakyi 59, 63–4, 79, 85, 95–6
  oswaldi 17, 58, 85–6, **95**, 96
    mariae 96
    olduvaiensis 96
  serengetensis 6
  age of sites 70–4
  axial skeleton 38–9
  body-weight 74–6
  carpus 49
  diet, adaptations 111–5
  diversity, intrageneric 75–87
  evolutionary sequence 84*
  femur 39–42, 40*, 49–50, 60–1
  fibula 42
  forelimb 29–38, 46–9
  habitat 99–102
  hind limb 38–43, 49–54
  humerus 30–4, 30*, 33*, 46, 49, 59–60
  metacarpus 49
  metatarsals, metatarsus 51–4, 53*, 54*, 61–2, 64
  motor habits, anatomical indications 102–11
  natural history 97–115
  pelvis 39, 69?
  phalanges 53*, 54, 55*, 62–3
  phylogeny 75–94
  radius 34*, 34–6, 49, 60, 70
  relationships 87–94
  robusticity quotient 75*, 76
  sacrum 38–9
  scapula 29–30, 46

  - size 74–5
  - skulls 8–20, 22, 44–5, 56–9, 63–5, 67–8, 70
  - stature 74
  - tarsus 42, 50–1, 51*, 61
  - taxonomy 94–7
  - teeth 20–9, 45–6, 47*, 48*, 59, 63, 65–6, 67–70, 89*
    - dimensions 28–9, 76, 78*, 80*
  - tibia 42–3, 50
  - ulna 35–8, 37*, 39*, 49
- *Sinkiangichthys longipectoralis* **290**
- sinuses, *M.o.* **495**, 495*
- Siphonales **358–9**
- Sirenia, gen. nov. 521–2, 524
- Sirte Basin 517–8, 520*
- Sivatheriidae 521
- Siwalik Formation 424
- skull, *M.o.* 485, **487–98**, 488*, 489*, 490*, 491*, 492*
  - measurements 502
  - mechanics of 505*
- skull, *P.m.* 381, **383–5**, 404; see also individual bones
  - post-ethmoid part of 389*
  - undersurface 385*
- skull-roof, *P.m.* 382*, 383, 384*, 385
- *Solenopora* 358
- South Africa, Triassic fishes 233–354
- *Spathognathodus* 128, 143, 147–8, 153, 157, **211–6**, 221
  - **abruptus** 127, 135, 138, 143, 148, 150*, 151, 153, 157, **211–2**, 215, 228; pl. 4, figs. 6–7
  - cf. *abruptus* 150*, 212; pl. 4, fig. 8
  - *celloni* 134, 197, 212
  - sp. ex aff. *celloni* 197
  - *comptus* 157
  - *elibatus* 157
  - **gulletensis** 127, 138, 141, 143, 150*, 151, 153, 158, **212–3**, 215, 218; pl. 4, figs. 9–12
  - *hassi* 135, 138, 141, 148, 150*, 151, 157, **213**, 214, 229; pl. 4, figs. 2–3
  - *inclinatus* 150*, 151, 160, **213–4**, 229; pl. 4, figs. 15–16
    - *inflatus* 216
  - *manitoulinensis* 157, 212
  - *oldhamensis* 133, 135, 138, 141, 148, 150*, 151, 157, **214**, 215–6, 229; pl. 4, fig. 1
  - cf. *oldhamensis* 213
  - *pennatus angulatus* 197, 209
    - *pennatus* 197
    - *procerus* 197
  - *polinclinatus* 150*, 151, 158, **214–5**, 229; pl. 4, fig. 13
  - *primus* 211, 213
  - *ranuliformis* 138, 141, 150*, 151, 153, 156, 158, 212, **215**, 229; pl. 4, fig. 14; see also *Pterospathodus amorphognathoides–S. ranuliformis* assemblage zone
  - *tyrolensis* 157
  - n. sp. of Walliser 213
  - sp. A nov. 138, 150*, 151, 153, **215**, 216, 229; pl. 4, fig. 4
  - sp. B nov. 141, 150*, 151, 153, **216**, 229; pl. 4, fig. 5
- sphenoid, *M.o.* **493**, 493*
- spinal plate, *P.m.* 403–4, 403*, 405*, 406–7
- *Spinella yassensis*, see *Spirifer* (*Spinella*)
- spino-occipital nerves, *P.m.* 393
- *Spirifer* (*Spinella*) *yassensis* Limestone (Lower Devonian, Australia) 380, 382, 410*, 411–3
- Spitsbergen 391
- squamosal, *M.o.* **493–4**
- Stinchar Limestone (Caradocian) 360–1
- *Stricklandia* 128–9, 159
  - *lens intermedia*, *prima*, *progressa*, *typica*, and *ultima* zones 131
- *Stuertzaspis* 392 [footnote]
- submarginal plate, *P.m.* 398, 398*, 406
- subnasal shelf or lamina, *P.m.* 396
- suborbital plate, bone, *P.m.* 385, 390, 396*, 397, 406
- subpituitary fenestra, *P.m.* 390–1, 406
  - fossa, *P.m.* 391
- Suidae 521, 524
- Sulaiman Range 421–82
- supramaxillary canal, *P.m.* 397
- supraoccipital spine, *P.m.* 384, 395, 406
- supravagal process, *P.m.* 393
- Swartkrans 5, 5*, 69–70, 72–3, 73*
- *Synorichthys* 322, 347
- *Synprioniodina* 147, 216–7
  - *alternata* 216
  - *bicurvata* **216–7**, 230; pl. 5, fig. 28
  - *silurica* 157, 191, **217**, 230; pl. 5, fig. 72

- Taemas area, Australia, stratal subdivisions 410*
  - stage 410*
- *Tapinosteus* 388, 390, 395, 406
- Taylor, Dr S. W. 517
- teeth, *P.m.* 386, 388
- telencephalon, *P.m.* 396
- Telychian 128, 130*, 131*, 141
- Teratodontidae 486
- terebratellacean brachiopods 371–2
- *Teredo* 518
- Ternife 5, 5*, 73–4, 73*
- testudinid 521
- *Textularia martini* 432
- *Thalarctos* 504, 507
  - *maritimus* 504
- thallus, progressive elaboration of, in Dasycladaceans 370–1
- *Theropithecus* (*Simopithecus*) 1–123 *passim*, **94–7**; see also *Simopithecus*
  - *brumpti* 86
  - *darti danieli* 47*, 48*, 86, 93, **97**
    - *darti* 47*, 48*, 69, 84*, 86, 95, **96**; pl. 16, figs. c, d
  - *gelada* 4–10, 5*, 12, 14, 17–18, 22, 29, 31–2, 33*, 35–9, 39*, 41–3, 47*, 48*, 49–54, 51*,

53*, 55*, 57, 60, 62–3, 65, 68–9, 74, 76, 81, 83–5, 84*, 88*, 89*, 91*, 93, **94–5**, 98, 102–9, 102*, 103*, 107*,108*, 112–3, 115; pl. 1, figs. c, d
  teeth, dimensions 11*, 13*, 23–8, 78*, 80*
olduvaiensis 86
oswaldi hopefieldensis 86
  leakyi 47*, 48*, 59, 63–4, 86, 88*, **96**; pl. 16, figs. a, b
  mariae 47*, 48*, 51*, 53*, 86, **96**, 102, 103*, 107*, 108*, 111; pls. 18–20
  oswaldi 47*, 48*, 84*, 86, 88*, 91*, **95**, 100, 102–4, 102*, 103*, 112; pls. 3–13
  subsp. pls. 14, 15, 17
wellsi 86
cheek-teeth dimensions 23–8
cranial dimensions 22
known occurrences fossil 5*
molars 20
taxonomy 94–7
Ticklerton, Ticklerton Brook 141, 226–7
Tityosteus 380, 408
Tomistoma dawsoni 521
Toombs, H. A. 377–419
  collections by 379–80
  localities of 380, 411–4
Tortworth, Gloucs. 143, 226–7
Tragulidae 521
Triassic redfieldiiform and perleidiform fishes, South Africa and New South Wales 233–354
Trichognathus excavata 218
  prima 217
  symmetrica 219
Trichonodella 147, **217–20**
  aborflexa 218
  asymmetrica **217**, 230; pl. 7, fig. 17
  brassfieldensis 176, 210
  carinata 211
  edentata 210–1
  excavata 158, 182, **218**, 230; pl. 7, fig. 20
  ? *expansa* 157, **218–9**, 230; pl. 7, fig. 14
  inconstans 191, **219**, 230; pl. 7, fig. 16
  prima 217
  symmetrica 157, **219–20**, 230; pl. 7, figs. 15, 18, 19
trigeminus, *P.m.* 392
trionychid 521
Triploporella 368–9
  sp. 376, 377*
Truncorotalia broedermanni 453
  wilcoxensis 469
Truncorotaloides 426, 430, **470**
  collactea 443, **470**; pl. 7, figs. 13–15
  rohri 430, 463, **470–1**; pl. 6, figs. 11–12; zone Fig. 3, 427, 430–42, 446–9, 454, 464–5, 470–1, 474–6
  topilensis 429, 463, **471**; pl. 6, figs. 9–10; zone see *Globorotalia crassata*
Turborotalia centralis 454
Turseodus dolorensis 331, 332*

Ursus 504, 507
  arctos 503–4

vagus nerve, *P.m.* 393, 406
vascular plexus, sub-cutaneous, *P.m.* 392–3
Velebitella 371
vena posthyoidea lateralis of *Kujdanowiaspis* 392
Vermiporella 358, **360–1**, 371
  acerosa 361
  affluens 361
  borealis 361
  cf. *borealis* **361**; pl. 5, fig. 1
  canadensis 361
  eisenacki 360–1; pl. 3, figs. 1–2
  fragilis 360
  inconstans 361
  wesenbergensis 361
  sp. **361**; pl. 5, fig. 3
  sp. of Eisenack 360
  sp. of Høeg 361
vomer, *M.o.* 491

Wales, Llandovery outcrops 129*
Warroo Limestone 383, 410*, 412–3
Watsonichthys 243
Watsonulus eugnathoides 345
weight of *M.o.* **503–4**
Welsh Borderland, Llandovery conodonts from 125–231
  Llandovery outcrops 129*
Welshpool 135, 226–7
Wenlock Edge 137*, 138, 141, 226
White, E. I. & Toombs, H. A. 377–419
White, M. E. 517
Wianamatta Group 237
Williamsaspis 402, 404, 407
wood, silicified 518, 520
Woolhope 143, 226–7

'Y' (hypothetical colobodontid ancestor) 333–5, 334*, 342

Zambia, see Lunsempfwa Valley
Zarafa zelteni 521
Zinjanthropus 71